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CONTRIBUTIONS TO THE HISTOGENESIS OF THE CARYOPHYLLALES. I.

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The purpose of the following paper is three-fold: 1, to set forth the results of a series of investigations upon the origin and structure of meristematic tissues, and their primary derivatives; 2, to accumulate additional evidence concerning the different phases of present histological, and histogenetic problems; 3, to furnish some considerations for the evaluation of anatomical characters in taxonomy. For many reasons, the order Caryophyllales presents a peculiarly favorable field for these researches. Its comparatively low position among Dicotyledones leads to the expectation that here will be found, to a certain extent, the instability of specializations and differentiations characteristic of low grades of development. The great diversity of morphological characters, moreover, would seem to bespeak concomitant extremes in histogenetic differentiations. Finally, on the other hand, the considerable community of habit throughout the group would tend to produce results quite opposite to those effected by the first two causes. Thus, as is always the case, the resultant of these and other forces would be expressed by the degree of departure of cell-aggregates, and of tissue-systems from a theoretical type. The theoretical reality, but practical non-existence, of this type will be made evident in the course of exposition.

To obviate the necessity of frequent repetition of subject matter, it has seemed best to subdivide the text into three parts. The anatomical and histogenetic details, except such as are common to all Dicotyledones, will be brought out in connection with one of the parts. Thus, while each part will concern itself chiefly with the elucidation of some particular problem in

histogeny, there will be found woven in with this the minute anatomy of the organs under discussion. The three subdivisions are as follows:

- I. The transition from root to stem.
- II. The origin and development of radicles.
- III. The apical growth of the stem.

I. THE TRANSITION FROM ROOT TO STEM.

Since the present paper lays no claim to originality in the general facts presented, but only in the particular application of these facts, it has seemed best to give a brief résumé of the principal researches as yet published upon this question. This historical account will be followed by an exposition of the type-structure of the hypocotyl; following this will be found the details of structure, and of transition in the various families of Caryophyllales. After a comparison of the different types of transition, will be given the conclusions deduced from the data presented.

HISTORICAL.

In the beginnings of plant anatomy, the transition-region was regarded as a geometrical plane, and its supposed position was determined by external data. Lamarck, Saint-Pierre, De Candolle, and Saint-Hilaire looked upon it as a line determined on the one hand by what is now called positive geotropism, on the other by negative. De Candolle, in particular, considered the transition-region to be not an actual organ, but merely the limit between two organs. However, he avoided two mistakes into which his successors fell. He located the transition below the cotyledons, and stated that rarely, if ever, was there any external evidence of its position. Saint-Hilaire and Meyen adopted the views of De Candolle, though the former fell into the error of regarding the constriction in the hypocotyl of some plants as an external indication of the location of the transition-region. Gaertner, Richard, Mirbel, and others thought the transition-region identical with the insertion of the cotyledons, while Cauvet believed it to be equivalent to the radicle.

Clos was the first to advance the theory that the "collet" was not a plane limiting two organs, that it was a distinct region determinable by morphological and histological characteristics. Confining himself mostly to the former, he defined the "collet" as that portion of the hypocotyl, limited above by the cotyledons and below by the area of root-hairs. That these alone are insufficient to accurately delimit the "collet" has since been shown by Van Tieghem, and by Gerard. Still, to Clos belongs the credit of having first discovered the real nature and extent of transition. Moreover, although Clos has left us no exact data concerning histological changes in the transition-region, he recognized the presence and importance of such, as the following passage will show. "Although Hugo von Mohl has proved that the vessels of the stem traverse the 'collet', as De Candolle understands it, without undergoing interruption, it is none the less true that it is in the 'collet' (as we have defined it) that the pith begins. It is in the 'collet', moreover, that the fibrovascular bundles, descending from the stem, unite in diverse manners, and undergo modifications, which determine for the root this or that rhizotaxic type. Also, the 'collet', in as much as it is an intermediary organ, partakes sometimes more of the anatomy of the root, sometimes more of that of the first internode of the stem, and and sometimes, finally, it has anatomical characters entirely peculiar to itself".

Van Tieghem, in 1869, first considered the "collet" to be a geometric plane, not entirely dissimilar to a node. His investigations, however, were correct; the cause of error was generalization from an insufficient number of data. As a result of careful anatomical research, he was able to add greatly to Clos' results by defining the "collet" as the organ, "where takes place the passage of xylem strands from alternation to simultaneous semi-rotation and superposition, by which they become centrifugal instead of centripetal, and where occurs the cessation of special conjunctive tissue, which is replaced by primary parenchyma". In 1872, Van Tieghem reversed his opinion concerning the abrupt transition from root to stem, giving for

the first time the precise details of the process. According to these later investigations, he divides the transition into four stages: 1, rotation of the xylem strands, which become centrifugal instead of centripetal; 2, their superposition upon the phloem strands; 3, the abrupt interruption of the pericycle without the latter; 4, the dilatation of the central cylinder, with the interposition of the conjunctive tissues. As Gerard has since demonstrated, and as will be brought out in the present paper, the sequence of these stages is not necessarily correct, the fourth as a matter of fact most often preceding the first. Yet these four steps are essentially typical for all Dicotyledones, and it is chiefly in the matter of minute detail that the knowledge upon this subject has since been increased.

Dodel, in the same year, as a result of investigation of the transition-region in *Phaseolus*, communicated the discovery of two new facts, both of great importance, and of universal application. The first of these was the division of the primary strands during the transition, and the second, the assumption of an intermediate, tangential (secantial) position, as a result of the torsion of the radial bundles to become collateral. In 1876, Goldsmith confirmed Van Tieghem's results, extending them, however, so that the "collet," which all recent writers had understood as limited to the hypocotyl, was, in a considerable number of cases, found to be located above the cotyledons. Another important deduction reached by the same author was that there is no interrelation between the morphological characters of the seedling, and the histological characters of the transition-region.

Gerard, in 1880 and 1881, extended his investigations so as to include all groups of vascular plants: it is his researches that have laid the foundation for all future work upon the "collet." Not only did he corroborate and extend the essential facts as demonstrated by Van Tieghem, Dodel, and Goldsmith, but he accumulated a mass of details that must stand as classic upon this question. His conclusions are a succinct résumé, not merely of his own investigations, but of the antecedent researches, and warrant a full translation in this place.

“To summarize: the ‘collet’ as a geometric plane does not exist.

“There exists, between the stem and the root, a region, more or less extensive, according to the plant, in which the elements of the root, in ascending to the higher portions of the axis, are modified, displaced, and assume gradually the configuration, position, and importance which they possess in the stem.

“The transformation of each of these elements is independent of the modifications of the adjacent elements; it may be continuous, or it may take place at intervals more or less separate; sometimes slow, it is at other times extremely rapid. The transition may originate, indifferently, in one or the other element: the one which inaugurates the transition here, will be the last to be adapted to it there. It results from these facts: 1, that the ‘collet,’ anatomically speaking, viewed in its different aspects, and in several plants at one time, presents the most various expressions, incalculable in number; 2, that the transformation of the tegumentary system is unable to furnish any character for the delimitation of stem and root. The mutation of the epiderm is but one of the phases of the transition; it occurs at very diverse times.

“Taken in its largest dimensions, the ‘collet’ may originate in the superior portion of the radicle, and may terminate in the fourth internode, though it rarely exceeds the cotyledons. It can be entirely localized in the radicle; it may occupy a portion of this organ, and all, or part, of the caulicle; finally, concerning the caulicle alone, it may comprise the totality, or only a part of it. It is seen, then, with what caution one should employ the two terms, radicle and caulicle; convenient, it is true, in descriptive writing, but liable to give rise to false ideas concerning the structure of these two organs.

“Most frequently, the transition occurs gradually, and completely in the hypocotyledonary axis; but, when the elements of the root reach the cotyledons, and are entirely lost in them without having realized the caulinary type, there is an abrupt change at the base of the internode, since the epicotyledonary

axis always possesses the elements of the stem normally disposed.

“The extent of the ‘collet’ seems everywhere dependent upon the diameter of the plantlet. The greater this is, the more quickly the transition takes place; but it is necessary to add, that, beyond a minimum dimension, this cause seems to have no influence. The absence of the caulicle affects also the rapidity of the movements, and, consequently, the length of the ‘collet.’ This region is extremely short with the vascular cryptogams, and the monocotyledons deprived of this organ. An extensive pith in the root, facilitating the displacement of the elements, also renders the transition more rapid.

“There is no family character to be drawn from the study of the ‘collet.’ There is merely a certain constancy in the species; whatever the longitudinal development of the plantlet, the elements possess the same disposition beneath the cotyledons.”

Gerard's conclusions, well-founded and complete as they are, leave three very evident lacunæ: 1, concerning the constancy of transition-type and method for each species; 2, the reduction of the manifold forms of transition to a definite number of more or less well-defined types; 3, a determination of the concomitancy of transition types, and accepted diagnostic characters in the higher groups. It would be presumptuous in a paper so limited in scope as the present one to postulate final conclusions with reference to any of these questions. The Caryophyllales afford, however, much cumulative evidence, the import and weight of which will be hereinafter discussed.

GENERAL FACTS OF THE TRANSITION.

The tegumentary cylinder plays no part in the transition. The epidermis of the root, however, which is characterized by the possession of root-hairs, and by its rounded, irregular, loosely-disposed cells, undergoes very considerable modifications. It first loses its root-hairs; the cells increase in size transversely and their outer walls begin to cuticularise. Finally, they are reduced in number about one-half, they elongate radi-

ally, and become very firmly compacted together, so that outwardly they present a continuous, cuticularised surface. The exoderm undergoes at the same time corresponding changes. It gradually loses its property of suberisation, the cells decrease considerably in size; and ultimately become more or less collenchymatous.

The transformation of the epiderm, although a feature of the transition, is in no way, or at least indirectly alone, connected with the changes which occur in the central cylinder. In most cases, the transformation of the epiderm takes place completely, before the first step of the internal transition has occurred. In some instances, on the other hand, the internal transition is practically accomplished before the epiderm loses those features which characterize it in the root. Thus, it is readily seen that the epiderm and the central cylinder are practically independent of each other with respect to their behavior. As for the transformation itself, it may take place rapidly, or gradually; it may extend over a large, or a small portion of the hypocotyl.

The cortical cylinder is modified but little. The number of layers of cells ordinarily increases toward the cotyledons, and at the same time the size of the cells undergoes a consequent decrease. Their form frequently changes from polyedric to rounded, and the whole tissue becomes characterized more and more by intercellular spaces. The endoderm, also, suffers but slight changes. It loses its property of suberisation, the characteristic punctation disappears, and it becomes, toward the apex of the seedling, more and more amyliiferous.

The modifications which affect the pericycle are inconsiderable. In many plants, the pericycle persists from the tip of the root to the cotyledons without the slightest variation except in the number of cells. Even when it enters the cotyledons, which it does in company with the endoderm, and the entire cortical cylinder, it suffers no change. In some cases, however, there is a diminution in the size of the pericyclar cells situated in front of the phloem strands, and, not infrequently, some, or all the cells directly opposite the phloem disappear.

Although Gerard makes the distinct statement that the mesenchym is entirely passive, the evidences of its activity are so numerous as to make it impossible to accept such a conclusion. Its function is four-fold: 1, to bring about the separation of the xylem strand into two plates, and, sometimes, the subsequent disintegration of these; 2, to intervene between the prototracheids and the pericycle; 3, to give origin to the medulla of the central cylinder; 4, to originate the procambium.

While the mesenchym may be regarded as the causative tissue, it is the xylem that is chiefly concerned in the changes which occur in the central cylinder. The process by which the centripetal xylem of the root is transformed into the centrifugal xylem of the stem may be divided into five stages:

1. Duplication and equalization of the xylem elements.
2. Longitudinal segmentation of the xylem strand into two plates.
3. Approach of xylem and phloem.
4. Superposition of xylem upon the phloem in secantial orientation.
5. Mutation from secantial to collateral orientation.

The first stage takes place by the transformation of the adjacent cells of the mesenchym into tracheids, and the decrease in diameter of all the elements of the xylem. In the second, the cells of the mesenchym insinuate themselves between the central xylem elements, and, growing rapidly, force them apart into two plates. At the same time, the prototracheids are pushed back from the pericycle by the mesenchym, and they take part in the constitution of either plate. In the third stage the xylem plate, either as a whole, or in part, approaches the phloem, or in some cases, the movement appears to be mutual. In the fourth, the xylem is superimposed upon the cambium in face of the phloem. From linear, or plate-like, it becomes cuneiform, and passes quickly from the secantial orientation to the collateral, the fifth stage. In elongated, slender hypocotyls, the fifth stage is rarely reached below the cotyledons, and sometimes it is found just above them. In short, stout hypocotyls, it is usually found in the lower portion of the "tigelle",

the upper part of which then exhibits the structure of the stem proper.

Compared with that of the xylem, the behavior of the phloem is very simple. At the beginning of the transition, the phloem strands extend themselves along the pericycle. When the xylem splits, the phloem frequently divides also; sometimes, however, it remains entire, and division occurs only after the superposition of the xylem. In the assumption of the secantial orientation, the phloem is usually passive, though movement does sometimes take place in it, as well as in the xylem.

The cambium (procambium) is produced directly from the mesenchym. Its purpose is two-fold; to connect the xylem and phloem into the collateral bundle, and to originate, in most cases, the vascular strands of the first internode.

DETAILS OF STRUCTURE AND TRANSITION IN THE VARIOUS FAMILIES.

CARYOPHYLLACEÆ.

Dianthus sinensis. The tegumentary cylinder of the root occupies more than three-fourths of the diameter. It consists, besides the epiderm, exoderm, and endoderm, of a cortical parenchyma of three or four layers of rounded cells, with numerous very small intercellular spaces. The outer layer is usually the largest, and from it the adjacent layers gradually decrease in size, on the one hand toward the epiderm, on the other toward the endoderm. In some cases, contrary to Van Tieghem's and to Gerard's generalizations, the cells of the exoderm are the largest of the tegumentary cylinder. There is, then, an abrupt change to the numerous small cells of the epiderm, and a gradual transition towards the cells of the endoderm. The cells of the latter are prismatic; their walls are so closely applied to those of the pericyclar cells that intercellular spaces are nearly invisible, or utterly lacking (I:1).

The central cylinder possesses a simple, one-layered pericycle, composed of 25 to 30 polyedral cells. The stele is diarch, each xylem strand containing, ordinarily, four, rarely five or six, elements, the outermost of which, prototracheid, lies against

the pericycle. The two strands are united in the centre by a large tracheid, and the double xylem strand is thus a single row of elements for, at least, a large portion of the root proper. The number of rows in the rays of the mesenchym is regularly three. Where the mesenchym touches the pericycle, its cells alternate with the cells of the latter, and it is only to be distinguished from a second layer of the pericycle by the fact of its interruption by both prototracheids and protophloem. The two phloem strands consist of plate-like masses, extending the length of four or five pericyclar cells. They contain two sorts of elements, large primary sieve-tubes, alternating with the cells of the pericycle, and small, cuboidal or polygonal cells, scarcely separable from the mesenchym.

The first change in the structure of the root takes place in the epiderm and the exoderm. The manner and nature of this has already been pointed out. Its complete independence of any transformation in the central cylinder is evidenced by the fact that both epiderm and exoderm have practically assumed their ultimate expression, before there has been the least disturbance of the elements in the central cylinder (I:7,8).

At a distance of about three millimetres from the tip of the root, the cells of the mesenchym adjacent the large, central tracheid become lignified, and pass over into constituents of the xylem strand. At the same time, there is a considerable increase in the size and activity of the phloem strands. They may now become more or less broken up into two separate strands (I:2) or they may maintain their integrity for some time yet. About a millimetre above the increase of the xylem strands, the mesenchym grows in between the elements of the latter and forces them apart first into two more or less irregular plates (I:3), and finally, by continued intrusion, into a number of very irregular, isolated strands. Just previous to this, the mesenchym in face of the phloem strands has passed over into cambium, and the phloem itself, if still undivided, splits into a number of strands, which come to lie along the pericycle for a very considerable distance, ultimately being distributed here and there along almost the entire periphery (I:4).

The prototracheids, during these changes, assume a position more remote from the pericycle, and, with the adjacent xylem, form the xylem element of the bundle-trace of the cotyledons (I:5). These enter the cotyledons, with respect to the phloem strands which accompany them, in secantial orientation, which, however, passes over almost immediately into the centrifugal. In some cases the whole number of the xylem strands is carried into the cotyledons, and the fibrovascular strands of the first internode, the stem proper, arise from the residual phloem-cambium of the hypocotyl (I:6). In other instances, the fibrovascular strands, alternating with those destined for the cotyledons (I:5), enter the first internode, and, by division, give rise to the vascular system of the stem.

The transition-region extends, then, from the upper portion of the root proper to the cotyledons, and includes the whole of the hypocotyl above the collet, the "tigelle".

Silene armeria. The diameter of the tegumentary cylinder of the root is very variable. Near the tip, it consists of but four layers, epiderm, exoderm, one-layered cortical parenchyma, and endoderm. The transition in size takes place only toward the central cylinder, the exoderm alone equalling the cortical parenchyma and the endoderm in extent. In the vicinity of the collet the number of rows in the parenchyma increases to two or three, and the outer of these dominates the cylinder, so that decrease, as normally, takes place in two opposite directions, toward both epiderm and exoderm. The cells are now nearly orbicular, and the tissue of the entire cylinder is characterized by very numerous and regular intercellular spaces, which are entirely lacking in the root. The cells of the endoderm are more or less elongated transversely, so that, ultimately, they become prismatic.

The pericycle is simple and contains 25 to 30 polyedric cells. As in *Dianthus sinensis*, it persists up to the cotyledons, increasing the number of its cells to correspond to the expansion of the central cylinder: in face of the phloem strands, the pericyclar cells sometimes diminish in size, but apparently never wholly disappear. The composition and arrangement of xylem

and phloem are very similar to that already indicated for *Dianthus sinensis*. The xylem is diarch, and consists usually of nine elements, four in either arch, connected by a large, central one. The behavior of the xylem is quite different in different individuals. Ordinarily, the single-rowed strand persists until the region of transitional activity in the upper part of the root is reached. Frequently, however, at a very short distance from the tip, the xylem becomes two- or three-rowed, and the root maintains this structure until the collet is reached. The phloem, composed of both primary sieve-tubes and smaller accessory vessels, forms a columnar strand on either side the xylem, and separated from it by two rows of mesenchymatous cells.

The transformation of the epiderm and the exoderm takes place in the region of the collet, and is effected in a very short distance, being completed before modification of the central cylinder occurs.

As has already been pointed out, the xylem strand is frequently doubled in the lower portion of the root. When this is not the case, duplication occurs in the collet (II:1). In either instance, the real index of the beginning of the transition is to be found in the equalization of the diameter of the xylem elements, and the withdrawal of the prototracheids from the pericycle. Concomitantly, the mesenchym begins to grow vigorously, and those layers in front of the phloem strands pass over into the peculiarly cubical cells of the procambium. These changes take place less than a millimetre from the insertion of the cotyledons. The actively growing mesenchym pushes in between the xylem elements, and separates them first into two irregular plates (II:2). The phloem undergoes no important change, but simply extends itself further along the pericycle: the entire mesenchym, except that concerned in the disintegration of the xylem, and destined to become the pith, is transformed into procambium. The medulla soon appears in the center of the cylinder, and the xylem strands are separated into numerous secondary strands. The secondary xylem strands come to lie in four more or less definite, opposite groups

(II:3). The phloem apparently does not split into corresponding groups, but is, on the contrary, differentiated out of the procambium along the entire periphery. This condition, which is essentially that of secantial orientation, is attained a short distance below the cotyledons. By the time the latter are reached, the fibrovascular system is practically centrifugal. This is actually true, however, only for those strands destined for the first internode. Those which form the trace of the cotyledons are still slightly secantial, until the very moment of their entrance into the latter. The base of the first internode possesses a stele composed for the most part of procambium, but containing, also, the two vascular bundles received from the hypocotyl.

The transition-region, if the duplication of the xylem elements in the lower portion of the root may be excepted, begins scarcely more than a millimetre below the cotyledons, and terminates at the insertion of the latter.

Silene conoidea. The transition-region corresponds in the details of structure, location and extent so exactly to that of *Silene armeria*, that an exposition of it would be the merest repetition. The two species might well be one in so far as histological differences are concerned.

Silene otites. The transition region, though agreeing in the main with that of *Silene armeria* and *conoidea*, presents a few differences, which, though unimportant, are more or less constant. Among these is the very early appearance and abundant distribution of starch-granules in the endoderm (IV:3), a condition which takes place tardily and feebly in the other two species. The disintegration of the xylem strand occurs somewhat later also, and, in consequence, the stele has scarcely more than entered the secantial orientation by the time it reaches the insertion of the cotyledons (IV:4). The centrifugal arrangement of xylem and phloem takes place, then, at the very moment of entrance into the cotyledons, as was seen sometimes to be true in *Silene armeria*. The strands of the first internode have at this time, though little differentiated, already assumed collateral orientation.

According to Gerard's exposition, the details of transition in *Silene inflata* are in almost perfect accord with the facts already stated. The sole discrepancy is in the behavior of the phloem. In *Silene inflata*, it divides before passing into secantial orientation with the xylem; in *Silene armeria*, *conoidea* and *otites*, division of the phloem strands apparently never occurs. On the contrary, the procambium gives rise to accessory phloem, which forms, with the original strands, a more or less continuous circle within the pericycle.

In *Lychnis githago*, Gerard found the facts to be practically the same, with the exception of an additional step, consisting in temporary fusion of the strands during secantial disposition.

In the six species of Caryophyllaceæ investigated, the transition-region is based upon a single type of structure, the modifications of which are slight and of little importance. The transition-region, moreover, is always limited below by the collet; and above by the cotyledons, and, in most cases, is confined to the upper portion of the "tigelle" alone.

PORTULACACEÆ.

Portulaca oleracea. The tegumentary cylinder of the root occupies about three-fourths of its diameter. Besides the epiderm, exoderm and endoderm, it consists of a one-rowed cortical parenchyma, a condition which persists even to the cotyledons. The exoderm is uniformly composed of larger cells, and transition in size is, in consequence, regularly unilateral, i. e., towards the endoderm. The tissue of the cylinder is very compact, the cells are for the most part polygonal, and the intercellular spaces none. The cells of the endoderm differ considerably from those of the other layers in their elongated, prismatic form, as seen in transection.

The pericycle is one-layered, and contains usually about 25 cells. The cells in face of the phloem strands decrease greatly in size, especially upwards in the stem, and, before the cotyledons are reached, they disappear entirely. The stele is diarch, each xylem ray consisting usually of three elements, united in the centre by means of one large vessel. The prototracheids

lie directly against the pericycle. The phloem strands are more or less convex; and consist, in the lower portion of the root, of but six or eight elements, slightly differentiated from the mesenchym. The latter is composed regularly of two rows of cells.

The modification of epiderm and exoderm occurs at the very base of the "tigelle," while the structure of the stele is yet typical. It is rapid and is completed in a rather short distance.

As usual, the first indications of the transition are to be found in the conversion of adjacent cells of the mesenchym into xylem elements (V:1). The duplication of the xylem is never carried far, resulting almost always merely in the formation of a double-rowed xylem strand. At the same time equalization of the size of the elements occurs, and concomitant with this, the division of each phloem strand into two, resulting in the formation of four secondary strands, which assume a quadrate position (V:2). The cells of the mesenchym now penetrate the xylem strand, separating the metatracheids from the prototracheids, but leaving the xylem grouped generally into two plates (V:3). Simultaneously, the interposition of mesenchym between pericycle, and prototracheids takes place. The pith grows rapidly in the centre of the cylinder, and either xylem plate is forced back upon the two secondary phloem strands, which have grown toward each other, and have united (V:4). The interposed mesenchym is meanwhile converted into procambium. Alternating with the two bundles thus formed, are two large strands of procambium, arising from the modification of the mesenchym. Thus, the whole of the xylem and phloem elements of the hypocotyl is concerned in the fibrovascular strand of the cotyledons (V:5). Just below the cotyledons, each of the procambial strands divides into three parts, each of which is differentiated into a fibrovascular bundle, and as such enters the first internode. The orientation of vascular strands is, thus, typically collateral just below the insertion of the cotyledons, and the transition-region is bounded above by the latter.

Portulaca oleracea differs from all Caryophyllaceæ (except

sometimes *Dianthus sinensis*) investigated, in the constitution of the fibrovascular bundles of the cotyledons by the entire vascular portion of the stele; from all but *Silene inflata* (rarely *Dianthus sinensis*), in the division of the phloem strands.

NYCTAGINACEÆ.

Allionia hirsuta. The tegumentary cylinder is especially broad, the number of layers in the cortical parenchyma is ordinarily five or six. The cells of the layer next within the exoderm are the larger; from these inward, the decrease in size toward the small endodermal cells is very gradual, toward the epiderm, it is abrupt. The cells of the tissue are globose, and the tissue itself is characterized by numerous, small intercellular spaces. The cells of the endoderm are almost perfectly globose in shape, and early undergo cuticularisation.

The pericycle is simple and consists of about 40 cells. These persist without noticeable modification throughout the root. The stele is diarch, rarely pseudo-tetrarch. In its simplest expression, it is but a single row of vessels, of which there are five in each arch, a large central one serving to unite the two archs. This condition is found for the most part only near the tips of roots. In most cases the xylem strand is two-rowed (VI:1). The centre of the cylinder is occupied by a very large tracheid, about which is grouped a circle of similar, smaller elements, which are continued bilaterally into an arch consisting of six or seven tracheids. Such a strand is, of course, nothing but an anticipation of duplication: its constancy lends especial significance to it, however. The prototracheids do not touch the pericycle, but lie against certain cells, which seem to indicate a double-layered pericycle at these two points. The mesenchymatous rays are very broad; they consist of seven or eight rows of regular, polygonal cells. The phloem strands comprise three rows of cells; the inner cells are small and scarcely distinct from the mesenchym, the outer are large and globose. They lie, for the most part, directly against the pericycle and constitute the primary sieve-tubes.

Contrary to what has been noted heretofore, the mutation of

the epiderm does not precede the disturbance of the elements in the stele, but is subsequent to it. In fact, the peculiar, non-cuticularized epiderm has undergone little modification by the time the transition from root to stem is really completed.

From what has been said above, it follows that duplication and subsequent equalization of the xylem elements is not the first indication, nor necessarily an indication at all, of the beginning of transition. The thickening of the walls of the central xylem elements disappears, "runs out", and simultaneously appears the intrusion of the mesenchym. The central elements are burst apart, and the xylem separates into two plates, for the most part transversely, but also somewhat obliquely (VI:2). By the further growth of the mesenchym, these plates are separated into four xylem strands (VI:3), of which the prototracheidal ones, though destined to disappear, serve to mark the trace of the primary bundles descending from the first internode. The other two strands, forced further and further back by the growing medulla, come to lie near the phloem plates, each of which has begun to divide (VI:3). Each of these two xylem plates now divides to form three, the middle one of which is like the prototracheids, marked for disappearance, while each outer one assumes a position near its corresponding, secondary phloem strand (VI:4). At the same time, the mesenchym in front of the phloem is transformed into cambium, the tracheids pass from the secantial disposition to a point directly in face of the cambium, and the bundles become collateral (VI:5).

The entire transition has taken place in that region of the hypocotyl, the collet, where occurs the abrupt change in the diameter of the seedling. The whole of the "tigelle," then, possesses the structure of the stem proper. It is characterized by four collateral bundles, which a short distance below the cotyledons are increased to six, by the appearance of the two primary bundles of the first internode, which arise directly above the disappearing prototracheids (VI:6). Imbedded in the pith at either end, still persist some of the tracheids of the vanishing middle strand of the xylem mentioned above.

Allionia nyctaginea. The structure of the root, and the structure, location and extent of the transition-region present no appreciable difference from the structure of the same organs in *Allionia hirsuta*. The points of correspondence are practically perfect for every stage.

According to Gerard, the transition-region of *Mirabilis jalapa* corresponds in every detail with the statements made above for *Allionia hirsuta*, and *nyctaginea*. He considers, however, that the total disappearance of the residual tracheids marks the termination of the transition-region. This conclusion seems to be entirely unwarranted; the persistence of the unused tracheids is more or less accidental, and has no particular significance. If Gerard's view were to be regarded as correct, the term transition-region, would be applied to a portion of the hypocotyl, the upper three-fourths of which is characterized by perfectly collateral bundles; manifestly a misapplication.

The transition-region of the Nyctaginaceæ, compared with that of the Caryophyllaceæ, occupies but a small extent of the hypocotyl. It is located uniformly in or near the collet, and often is almost entirely confined to it. The transition may be regarded as belonging to another type, characterized by the fact that the prototracheids, or their trace, enter the first internode, and not the cotyledons, as is the case in Caryophyllaceæ and in Portulacaceæ.

AMARANTACEÆ.

Amarantus retroflexus. The cortical parenchyma of the root comprises two or three rows of which the outer, as usual, is the larger. The exoderm differs but slightly from the outer layer, and, in fact, the two are often confluent. The tissue of the tegumentary cylinder is composed of globose cells, between which there are numerous, irregular intercellular spaces. The cells of the endoderm are very similar.

The pericycle is simple and contains usually about 20 polygonal cells. Those in face of the phloem undergo a very considerable diminution in size, while, in the upper part of the

hypocotyl, they disappear entirely. The xylem strand is diarch; each arch is composed of three or four elements, the outermost of which lies against the pericycle. The mesenchym is three-rowed and passes insensibly into the phloem strands. The latter are more or less cuneiform, and are composed of about twelve elements.

The transformation of the epiderm takes place, as is usual for slender hypocotyls, before the beginning of the transition. In the present case, the complete modification of the epiderm results long before the first change occurs in the central cylinder.

The transition is inaugurated by the duplication of the xylem elements and their subsequent equalization (VIII:2). The thickening of the walls of the mesenchymatous cells is only partial, however, and the next stage follows so quickly that, when the mesenchym appears in the centre of the cylinder, it ordinarily divides a single-rowed xylem transversely into two plates (VIII:3). Simultaneously, the prototracheids leave the pericycle, and each phloem strand undergoes division (VIII:3). Following this, a strand of procambium is developed from the mesenchym on either side in the space left by the separation of the secondary phloem strands. Each xylem arch is now further split up by the mesenchym, several elements assume a position in front of either phloem strand, the cambium appears, and the vascular strands take up the secantial orientation (VIII:4). During this process, the pith has made its appearance in the centre of the cylinder. Meanwhile, also, the procambial strands have developed into perfectly collateral strands destined for the first internode. Just below the cotyledons, the xylem of the strands in secantial orientation turns upon the phloem, and seeks to take up a centrifugal position (VIII:5). This step, however, is rarely accomplished before the strands enter the cotyledons, where they assume the typical collateral disposition.

In some hypocotyls, the strands reach the cotyledons even before they have taken up the secantial disposition. In such instances, the phloem and xylem, both still centripetal, enter the

cotyledons, and are there properly oriented. The mesenchym, then, early develops the lateral, procambial strands, and these enter undifferentiated, the first internode, where they are quickly converted into primary vascular bundles. In such individuals, there is always an abrupt transition from "tigelle" to stem at the insertion of the cotyledons.

Whether the transition be gradual, as is normally the case, or abrupt, as just described, the whole of the xylem, and generally the entire phloem, passes into the cotyledons. The trace of the first internode is formed, then, by the conversion of the interfascicular mesenchym into procambial strands. More infrequently, each phloem strand, instead of dividing into two secondary strands, splits into three, and the middle one of these is differentiated into a vascular strand of the first internode. The six vascular strands of the second internode are formed by the splitting of each of the primary strands of the first internode into four, three of which enter each cotyledon, while the fourth passes into the third internode.

As has been found elsewhere to be the case in species of the same genus, *Amarantus albus* presents no material points of difference in the details of the structure of the seedling.

The manner of transition in *Amarantus paniculatus*, according to Gerard, is in perfect accord with the second method described for *Amarantus retroflexus*. In consequence, *Amarantus retroflexus*, *albus*, and *paniculatus* are characterized by exactly the same type of transition-region, notwithstanding the fact that this type shows slight modifications in different individuals.

The transition-region in *Amarantaceæ* begins, then, in the upper portion of the "tigelle", a considerable distance above the transformation of the epiderm, and is terminated by the cotyledons.

CHENOPODIACEÆ.

Beta alba. The tegumentary cylinder occupies four-fifths of the diameter of the root. Besides the epiderm, exoderm, and endoderm, it possesses a cortical parenchyma, composed

of five or six rows of cells. The middle row is the largest, and the diminution of successive layers toward both epiderm and endoderm is gradual. The cells are irregularly polygonal, and the tissue abounds in regularly rounded intercellular spaces. The endoderm is composed of compact, cuboidal cells.

The pericycle is simple and comprises usually about 40 cells. The pericyclar cells, though diminishing in size above in face of the phloem strands, persist until they reach the cotyledons, which they enter along with the cortical cylinder. The xylem is diarch, each arch consisting of four or five elements, of which the prototracheids, indifferently, lie against the pericycle or remote from it. The mesenchym is broad and contains four or five rows of regularly polygonal cells. The phloem strands are large plates, extending for a considerable distance along the pericycle. They are four- or five-rowed, and comprise two sorts of elements. The inner rows consist of small cells scarcely separable from the mesenchym, the outer row is composed of large, primary sieve-tubes, which lie against the pericycle.

The transformation of the epiderm occurs in the upper part of the root, only a short distance below the duplication of the xylem elements.

The increase in number of elements in the xylem, and the equalization of their diameter takes place in the middle of the collet (IX:2). Concomitant with this, the layers of mesenchym adjacent to the phloem pass over into procambium. The mesenchym then forces itself in between the xylem elements, and the metatracheids are separated from the original strand (IX:3). By the further intrusion of mesenchym, the xylem is split into two secondary strands, which are pushed back toward the periphery. At the same time, each phloem strand divides, and the two resulting parts become somewhat widely separated (IX:4). The stele reaches the cotyledons in this condition, and the xylem and phloem strands pass directly into the seed-leaves, where they assume their proper disposition. More rarely, the phloem strands on either side the xylem become con-

fluent along the pericycle, and the xylem and phloem then enter the cotyledons in secantial orientation. The mesenchym, which grows in between the secondary strands of the phloem, is transformed into procambial strands, which, above the cotyledons, are differentiated into the primary bundles of the first internode. Thus, the whole of the vascular elements of the stele passes into the cotyledons.

Chenopodium album. The cortical parenchyma is ordinarily three-rowed, the outer row is the largest, and the others decrease gradually toward the endoderm. The latter is composed of rounded, close-fitting cells, very much smaller than those of the inner layer of the parenchyma. The pericycle is simple, and is composed of about 20 cells. It persists with but little change, apparently, throughout the hypocotyl. The xylem is diarch, each arch containing three or four elements. The prototracheids lie directly against the pericycle. The mesenchym is two-rowed; it passes gradually into the inner row of the phloem strand. The latter possesses two or three primary sieve-tubes, lying against the pericycle (X:1).

The transformation of the epiderm takes place in the upper part of the root, some distance below the collet, and several millimetres below the beginning of the transition.

The duplication of the xylem begins three or four millimetres, or more, below the cotyledons. At the same time, the separation of the prototracheids from the pericycle takes place (X:2). Some distance above, the mesenchym grows in between the xylem, dividing it into two strands. Concomitantly, the division of the phloem strands, and the subsequent separation of the secondary strands occurs. The ends of the secondary xylem strands approach the secondary phloem strands, and the transition from the secantial to the collateral orientation begins (X:3). In the early steps of this process, the fibrovascular strands for the first internode are cut off and quickly assume the collateral disposition. The passage of the bundles destined for the cotyledons from centripetal to centrifugal is laborious, and requires considerable time. It is accomplished by the gradual approach of the secondary phloem strands, and by

the swinging toward each other of the xylem plates upon the prototracheids as a pivot. Just before entering the cotyledons, the two adjacent bundles become confluent, and enter the cotyledons as a simple vascular strand. Simultaneously, the strands passing upward into the internode undergo division in rapid succession, so that the first internode possesses twelve vascular strands, three toward either face. Six of these, the three on either side, which alternate with the cotyledons below, pass into the leaves of the first internode; the remaining six enter the second internode, where they again undergo division.

Contrary to Gerard's conclusions upon the effect of the diameter and length of the hypocotyl upon the rapidity of transition, *Beta alba*, with a short, thick hypocotyl, possesses a truncated transition-region, and the vascular elements of the stele are forced into the cotyledons long before they have assumed the customary arrangement. In *Chenopodium album*, on the contrary, where the hypocotyl is exceedingly slender and elongate, the transition is perfected, and the "tigelle" has the structure of the stem before the insertion of the cotyledons is reached.

Atriplex hastata, investigated by Gerard, is intermediate between the two plants studied above: the vascular elements of the stele pass into the cotyledons while in secantial orientation.

PHYTOLACCACEÆ.

Phytolacca decandra. The tegumentary cylinder occupies nearly two-thirds of the diameter of the root. The cortical parenchyma consists of three or four layers of almost uniform size; toward the endoderm, the cells become slightly smaller. The latter are polygonal, and the tissue is compact, and almost without intercellular spaces. The endoderm is not at all distinctive; it is simply the inner layer of the cortical parenchyma.

The pericycle is simple at first, comprising about 40 cells. In the upper part of the root, however, it undergoes division to form a sort of procambial tissue, and it maintains this condition until it enters the cotyledons. The xylem is diarch: each arch consists of five to eight elements. The prototrach-

eids usually lie against the pericycle, but this is not necessarily true. The mesenchymatous rays are broad, and contain five or six rows of cells. The phloem strands are characteristic; they are composed almost wholly of eight to twelve large primary sieve-tubes.

As has already been demonstrated for those plants which experience an abrupt change of diameter in the colletal region, the transformation of the epiderm occurs comparatively late. In *Phytolacca decandra*, the epidermal cells finally acquire the characteristics of the epiderm of the stem a short distance above the collet. This external change corresponds internally with the appearance of the medulla in the central cylinder.

The duplication of the xylem strand occurs in the upper portion of the root, not far below the collet (XI:1). About one millimetre above this point, the mesenchym intrudes itself between the xylem, and the latter is divided transversely into two equal, secondary strands (XI:2). Shortly after, each secondary strand is again split into three, of which the middle one contains the prototracheids (XI:3). Concomitantly, the outer strands approach the phloem, the adjacent mesenchym is modified to form cambium, and the vascular elements of the stele assume the secantial orientation. The strands do not divide, but extend themselves along the pericycle and, together with the procambial strands developed from the mesenchym, form a circle of phloem elements, interrupted only in face of the prototracheids. The secondary xylem strands swing slightly away from each other, and tend to assume a more nearly collateral disposition. They enter the cotyledons, however, before this is accomplished, and the perfectly collateral arrangement is only realized there. The prototracheidal strands furnish the middle bundle of the cotyledons, and the outermost secondary strands, the lateral.

In some individuals, a peculiar modification of this method of transition is presented, which, in many respects, is identical with that demonstrated for *Allionia hirsuta* and *nyctaginea*. The xylem is first split into four alternating strands, two prototracheidal, and two purely secondary. The latter again

divide into three, the outermost of which assume a position near the phloem strands, which have already divided. The passage from the secantial to the collateral disposition takes place almost instantaneously. The stele now contains four collateral bundles, and alternating with these, four secondary, reduced xylem strands, and presents exactly the arrangement characteristic of *Allionia hirsuta* (VI:5) and of *Allionia nyctaginea* (VII:5). This disposition is maintained for nearly a millimetre: the two xylem strands, which were the middle ones formed by the splitting of the secondary xylem plates after the separation of the prototracheids, are, however, transformed into collateral bundles before the cotyledons are reached. Before entering the cotyledons they divide and one-half of each goes to either cotyledon, forming the outermost strand. Of the four original collateral bundles of the upper portion of the hypocotyl, two enter either cotyledon and form the principal strands. Central, between these two, still persists the prototracheidal strand, represented only by two or three spiral vessels.

Phytolacca decandra thus presents two widely different modifications of the one type of transition. The one first described appears to be the more frequent, the second, rather exceptional. That they are modifications of one type, and not two distinct types, is shown by the fact that, in both cases, the vascular elements of the central cylinder of the hypocotyl pass, in their entirety, into the cotyledons, while the fibrovascular system of the first internode is derived from the procambial stele, which enters it from below. More commonly, the elements of the hypocotyledonary stele reach the cotyledons before they attain their ultimate expression, and the transition-region is truncated. In rarer instances, and for reasons which are correlates of the individual development of each plant, the transition occurs in the lower portion of the hypocotyl, and, in consequence, the collateral structure of the stem characterizes the greater part of the "tigelle".

Gerard's investigations of *Phytolacca decandra* have led him to assign to it a method of transition for the most part in accord with what has been presented above as normal.

POLYGONACEÆ.

Polygonum lapathifolium. The tegumentary cylinder, in addition to epiderm, exoderm and endoderm, possesses a cortical parenchyma comprising five or six layers. The middle layer, or layers, is uniformly the largest, and the decrease in size of the other layers is very gradual toward both endoderm and epiderm. The cells are typically Maltese-cross-shaped, and the tissue is characterized by the large and regular intercellular spaces. The endoderm, on the contrary, is very compact, and its cells are cuboidal.

The pericycle is simple, and persists with slight modifications until the cotyledons are reached. The xylem is tetrarch. The archs are placed at right angles to each other, and consist usually of four elements, united in the centre by a larger one. The prototracheids lie directly against the pericyclar cells. The phloem strands are likewise four: they are more or less cuneiform, and are separated from the xylem rays by two or three rows of mesenchymatous cells (XII:1).

The transformation of the epiderm occurs in the upper portion of the root, while the typical disposition of the stelar elements is yet undisturbed.

Duplication of the xylem elements, and their subsequent equalization never occurs. The beginning of the transition is indicated by the disintegration of the central xylem element, and the appearance of the mesenchym in the centre of the cylinder. The rays of the xylem strand are separated from each other, and are pushed back toward the pericycle (XII:2). Shortly after, the phloem strands grow rapidly and extend along the pericycle until they reach the xylem. The phloem elements then group themselves about the xylem strands, and are, at the same time, crowded out midway between the xylem bundles by the mesenchym (XII:3). The bundles, or, rather, the masses of phloem and xylem, are still centripetal, and they

enter the base of the cotyledons with this disposition. The whole number of xylem and phloem elements pass into the cotyledons. In consequence, the stele of the first internode is formed by the modification of the internal mesenchym of the hypocotyl into procambium.

The transition-region of *Polygonum lapathifolium* commences in the collet, and terminates only in the base of the first internode.

Rumex altissimus. The features of the tegumentary cylinder are essentially similar to those already noted for *Polygonum lapathifolium*: the same is true of the pericycle.

The xylem is tetrarch, but the rays are of different value. Two, the primary, usually contain four elements and the prototracheids lie against the pericycle, while the alternate two, the secondary, comprise but two or three elements, which rarely attain the pericycle. The phloem is tetramerous, and, with the mesenchym, presents no points of contrast with the same structures in *Polygonum lapathifolium* (XIII:1).

The first stages of the transition concern the xylem alone. Duplication of the elements takes place in the upper part of the root, and the secondary rays of the xylem begin to disappear at the same time (XIII:2). This condition persists for a short time and is then followed by the equalization of the size of the elements, the disappearance of all but the primary ones and the prototracheids, and the ultimate arrangement of these in a single, radial series (XIII:3). During this time, the phloem and the mesenchym have remained passive. The mesenchym now intrudes itself between the central elements of the xylem, and, simultaneously, between the pericycle and the prototracheids. The xylem plates are then forced toward the centre of the cylinder, and the elements arrange themselves about the medulla more or less in the form of a V. Concomitantly, the opposite phloem strands, i. e., those separated by the uniseriate xylem plate (XIII:3), coalesce and the stele possesses now but two phloem masses, still separated by the mesenchym (XIII:4). This disposition is maintained without alteration until the cotyledons are reached, with the sole excep-

tion that the entire mesenchym of the stele is transformed into procambium, part of which becomes interfascicular cambium, and part, the originative tissue of the vascular system of the first internode.

The xylem and phloem masses reach the cotyledons without attaining the secantial disposition. At the moment of entrance, however, the phloem strands divide again into four, separated by the procambium. The two resulting vascular strands then assume the secantial disposition, and, one passing to either cotyledon, they are therein arranged according to the collateral type.

The final disposition of the vascular elements of the hypocotyledonary stele is the same in *Rumex* as in *Polygonum*. The method of attaining this, however, is very different. Instead of following the tetrarch type, the central cylinder assumes the diarch character, and the transition then occurs after the manner common to hypocotyls of this structure.

According to Gerard, the transition in *Rheum compactum* is different from that of *Rumex* or *Polygonum*. Not only do the four phloem strands divide to form eight, but each ray of the tetrarch xylem is split into two, resulting also in the formation of eight xylem strands. The secantial disposition is quickly passed through, each two adjacent vascular strands coalesce, and the "tigelle" attains the cotyledons characterized by four perfectly collateral bundles.

SUMMARY

Of all the various phases of the transition-region, there are four, which, by reason of their constancy within the species, and their great variation in higher groups, seem to be of essential significance. These are: (1) duplication of the xylem elements; (2) division, or non-division of the phloem; (3) the disposition of vascular elements upon entering the cotyledons; (4) the origin, or constitution of the cotyledonary trace. Of these, only the last, on account of its profounder significance, and greater constancy, is able to afford a satisfactory basis for the elaboration of certain types of transition. The other three,

by their not infrequent disappearance, or extensive modification, are unsatisfactory as fundamental characters for the analytical disposition of the manifold forms of transition. They are, however, of no inconsiderable service as cumulative characters, and may, moreover, be used as marks of subtypes.

The bundle-trace of the cotyledons may be constituted in three fundamentally different ways. It may be composed of the entire vascular system of the hypocotyledonary stele, holostelar; it may be constituted by those vascular strands, in which the prototracheids are the xylem elements, prototracheidal, or it may be formed from those bundles into which the metatracheids have passed, metatracheidal. The holostelar type is the most widely distributed. It is found in *Portulaca oleracea*, *Amarantus retroflexus*, *Amarantus albus*, *Beta alba*, *Phytolacca decandra*, *Polygonum lapathifolium* and *Rumex altissimus*. The prototracheidal trace is nearly as common as the holostelar: it occurs in *Dianthus sinensis*, *Silene armeria*, *S. conoidea*, *S. otites*, and *Chenopodium album*. The metatracheidal type is rare. Of the plants investigated, it exists in but two, *Allionia hirsuta* and *Allionia nyctaginea*.

Duplication is a very constant feature of transition. It occurs throughout the Caryophyllales, except in those possessing a tetrarch xylem strand, i. e., in *Polygonum* and *Rumex*. It is never found in *Polygonum*: in fact, the method of vascular formation renders it unnecessary, if not impossible. It takes place to a slight extent in the three individuals of *Rumex altissimus* investigated. The peculiarly anomalous transition of this species presents many puzzling features, however, and, until further research has determined these, the actual existence of duplication is more or less doubtful.

The division of the phloem, which is essentially, at least, a correlate of xylem division, is found in about half the species studied. It occurs in *Dianthus sinensis*, *Silene inflata* (according to Gerard), *Portulaca oleracea*, *Allionia hirsuta*, *A. nyctaginea*, *Amarantus albus*, *A. retroflexus*, *Beta alba*, and *Chenopodium album*. In *Silene armeria*, *S. conoidea*, *S. otites*, and *Phytolacca decandra*, the phloem strands, instead of under-

going division, increase greatly in extent, and finally occupy the greater part of the periphery. Naturally, this circle of phloem is broken up at the passage of the bundle-trace into the cotyledons; by this time, however, the process has lost whatever of significance it may have once possessed. In *Polygonum* and *Rumex*, there is no necessity for a division of the phloem, since the number of secondary xylem plates corresponds to the number of phloem strands. This is not strictly true of *Rumex*, since the secondary xylem rays disappear, leaving but two secondary xylem plates. In correspondence with this, however, the four phloem strands coalesce into two.

The vascular elements of the hypocotyl reach the cotyledons in one of three conditions, centripetal, secantial, or collateral. The first two are but varying degrees of expression of incompleteness, and may be classed together as truncated transition; the latter may, in contradistinction, be called complete transition. The three are, of course, nothing but various expressions of the same structure and are not essentially distinct. They vary not only from species to species, but, sometimes, from individual to individual. Truncated transition is found in *Dianthus sinensis*, *Beta alba*, *Polygonum lapathifolium*, and *Rumex altissimus*. Complete transition occurs in *Silene armeria*, *S. conoidea*, *S. otites*, *Portulaca oleracea*, *Allionia hirsuta*, *A. nyctaginea*, *Amarantus albus*, *A. retroflexus*, and *Chenopodium album*. *Phytolacca decandra* presents both truncated and complete transition.

The extent of the transition-region is quite constant for the Caryophyllales. It commences usually in or near the colletal region, and terminates, almost without exception, at the insertion of the cotyledons. In consequence, the transition-region and the "tigelle" are almost invariably coincident, and the latter possesses, then, a peculiarly distinctive structure. In *Allionia hirsuta*, *A. nyctaginea*, and in some individuals of *Phytolacca decandra*, the transition operates almost entirely within the collet, and the anatomical features of the "tigelle" are in no wise characteristic, but correspond to those of the stem proper.

To summarise:

The transition-region of each species is reducible to a constant type, which is, however subject to certain, non-essential modifications. The number of types of transition in the Caryophyllales is three: holostelar, prototracheidal, and metatracheidal. The correspondence of histogenetic, and taxonomic characters is insignificant and valueless, except in the species. Even here, it is general.

II. THE ORIGIN AND DEVELOPMENT OF RADICELS.

HISTORICAL.

Nägeli and Leitgeb, in 1868, were the first investigators to pay especial attention to the details of the development of radicels. The plants studied were *Pontederia crassipes*, *Oryza sativa*, *Veronica beccabunga*, *Lysimachia thyrsiflora*, and *Nasturtium officinale*. In these, they considered the plerome, and periblem to be derived from the pericycle, while the calyptra was regarded as a derivative of the endoderm. They paid little attention to the dermatogen, looking upon it, perhaps, as the inner layer of the calyptra. Although they found, in *Limnanthemum vulgare*, that the calyptra increased in thickness by the tangential division of the dermatogen, they interpreted the process incorrectly.

Reinke, in 1871, stated that the origin of the radicle was always endogenous, and that it took place in the pericycle. He followed very exactly the division of the pericycle into three layers, but he erred in concluding that the dermatogen was constituted by the upper layer resulting from the division of the pericycle into two, while the division of the lower layer gave rise to the periblem and the plerome.

Janczewski, in 1874, denied the correctness of Reinke's conclusions, and laid down the principle that the plerome alone was constantly derived from the pericycle. As a result of his investigations, he described five types of radicellar origin.

In the first type, *Pistia stratiotes*, the pericycle gives rise to the plerome and periblem, while the dermatogen and the calyp-

trogen arise from the division of the endoderm into two layers; in the second, *Alisma*, *Sagittaria*, and *Zea*, the plerome and periblem are derivatives of the pericycle, while the calyptrogen is formed by tangential division of the outer layer of the periblem; in the third, *Raphanus*, *Fagopyrum*, and *Helianthus*, plerome, periblem, and calyptrogen arise from the successive division of the pericycle; in the fourth, Papilionaceæ and Cucurbitaceæ, the plerome alone originates from the pericambium, the periblem is formed from the successive division of the endoderm, and the calyptrogen is produced from the terminal cells of the periblem; in the fifth, both periblem and plerome arise from the pericycle. In the case of *Fagopyrum*, Janczewski speaks of the endoderm as forming a continuous layer about the radicle, the epigen, but he lays no emphasis upon the fact, and regards it apparently as of no importance,

Vonhohne, in 1880, taking up the suggestion of Reinke that the exit of the radicle took place by the absorption of the tissue of the cortical cylinder, found that, as a result of chemical action, the cortical cylinder was digested and absorbed by the growing radicle.

Van Tieghem and Douliot, in 1889, in a memoir become classic, laid down the two fundamental principles, that the Dicotyledones present but a single type of radicular formation, albeit this may show secondary variations, and that the radicle always proceeds, in its entirety, and in a manner essentially the same, from the pericycle of the mother root. Van Tieghem, moreover, was the first to follow the absorption of the cortical cylinder to its logical conclusion, and to distinguish between radicles with "poche digestive" (epigen), and radicles without "poche digestive". He also investigated the position of the rhizogenic arcs and their relation to the elements of the central cylinder, and traced the detailed development of radicles from simple and compound pericycles.

THE ORIGIN AND STRUCTURE OF RADICLES IN GENERAL.

The point of origin of the radicle is determined by the disposition of the xylem strands within the root. In the case of

diarch xylem strands, the disposition of the rhizogenic areas, and hence of the radicles, is either diplostichous, or monostichous. Where the xylem strand is tetrarch, or polyarch, the arrangement of radicles is isostichous. In the latter, which admits of little or no variation, except in those plants possessing pericyclar canals, the middle cell of the rhizogenic arc is exactly opposed to the prototracheid, and the radicles stand at equal distances from each other. Of the polyarch types, the tetrarch is the most common, and isostichy comes to mean quadriseriation in nearly all cases.

In the case of a root possessing a diarch xylem strand, the radicles may be either quadriseriate, diplostichous, or biseriate, monostichous: between the two are numerous transitional modifications. In typical diplostichy, the radicle lies directly in face of the mesenchymatous ray, and its basal cells rest on the one hand upon the prototracheids, on the other, upon the primary sieve-tubes. From this, it results that one-fourth of the pericycle is concerned in radicular formation. When the quadrant contains an uneven number of cells, as is generally the case, the central one determines the axis of the radicle, and is the originative of the histogenic row: if the quadrant is composed of an even number of cells, the central two serve to determine the axis of the radicle.

In the majority of roots, however, the axis of the radicle is not in direct continuation of the mesenchymatous ray, but deviates from such a line, toward the xylem more frequently, but sometimes also toward the phloem. The angle of this deviation may be slight, in which case the quadriseriation of the radicles is not destroyed, or, on the contrary, it may be great, in which case the radicles tend to become more and more biseriate. In some instances, the angle of deviation reaches 45 degrees, and the radicle comes to be inserted upon the prototracheid, just as is the case in quaternary roots, though the radicles are now biseriate, or monostichous, instead of quadriseriate, isostichous.

The rhizogenic arc, then, is determined with reference to the above principles. It is constituted directly by the cells of

the pericycle when these are polyedric; if they are prismatic, each first undergoes division. In transection of the root, the rhizogenic area always appears as the rhizogenic arc, consisting of the cells of the pericycle concerned in the process.

The cells of the rhizogenic arc first elongate radially, and the central one or two divides transversely. Division follows quickly in the other cells of the arc, and the pericycle is then composed of two layers. The upper of these divides as did the pericycle, central cell first, lateral ones in quick succession. As a consequence, the young radicle consists of three layers, the lower, *plerome*, the middle, *periblem*, and the upper, *dermatogen*. The further development of each of these layers now devolves upon its initial cell, or histogen.

As a rule, the histogen of the *plerome* divides only transversely, and always in a basifugal direction. The segments also undergo transverse division for a short time, especially while the *plerome* is elongating rapidly, after which division is chiefly longitudinal. The formation of the pericycle of the *plerome* takes place usually by the longitudinal division of an apical segment of the histogen of the *plerome*. More rarely, the pericycle is developed from the ordinary segments of the histogen. The behavior of the dermatogenic histogen is essentially similar to that of the *plerome*. Its divisions are, however, always basipetal in direction. The first layer of the calyptra arises from the transverse division of the histogen of the *dermatogen*, and from the subsequent transverse division of the remaining cells of the *dermatogen*. Successive layers of the calyptra always arise below the first by the same process. As a consequence, the outermost layer, in which exfoliation always originates, is the oldest and the innermost, the youngest.

The histogen of the *periblem* divides almost invariably in a longitudinal direction. Ordinarily, one or two segments on either side of it share the same peculiarity for a certain length of time, so that the *periblem* is found to consist usually of but a single row of cells at the apex, while further down the sides, it is two-, or sometimes three-rowed. Both the lateral seg-

ments, and the histogen, however, divide ultimately to form either the endoderm and the exoderm of the cortical cylinder of the mature radicle, or their originative layers.

The exit of the radicle from the root was formerly supposed to result by the rupture of the cortical cylinder, caused by the rapidly growing tissue of the radicle. Van Tieghem was the first to deny this, and to point out the true method. He demonstrated that the process was a chemical one, in which diastasic solution and absorption of the adjacent cells occurred. He, moreover, divided radicles into two groups, according to the method by which this absorption took place. In some instances, the outer layer, or layers, of the radicle itself performs this function. In this case the calyptragen is often more highly developed for this process, though quite as frequently, solution and absorption of the circumjacent layers are carried on by the dermatogen alone. In other instances, the endoderm undergoes special modification to become a particular digestive organ. At the same time that the primary layers of the radicle are being formed, the cells of the endoderm undergo repeated radial division. In addition to this, the cells increase considerably in size, and are distinguished by the dense protoplasm and large nucleus. As the radicle grows, the accommodation of the transformed endoderm, or epigen, to it results by the appearance of new transverse divisions, and this peculiar digestive layer accompanies the radicle until the latter has penetrated the cortical cylinder, when it in its turn is digested and absorbed. In some plants, division of the endoderm takes place tangentially as well, and the result is a several-layered, or compound epigen, similar in behavior and function to the simple one.

As has been stated before, Van Tieghem is inclined to group radicles into two classes, based upon the presence or absence of the epigen. That this organ is purely local, if not sometimes, even, entirely accidental, is shown by the fact that it may exist in one of two nearly related genera, and be entirely lacking in the other. Even more; *Chenopodium album* sometimes possesses an epigen, and is at other times deprived of one.

Moreover, in the Chenopodiaceæ, especially, the epigen is a particularly variable, and inconstant structure. According to Van Tieghem, it is lacking in *Chenopodium album*, *quinoa* and *nitrariaceum*; in *Chenopodium*, when present, it consists of but four cells; in *Salsola tragus*, and *Acnida cannabina*, of but three; in *Beta maritima*, and *Kochia eriophora*, the epigen persists only until the middle of the cortical cylinder; in *Beta alba*, it is not absorbed until the radicle has made its exit, while in *Atriplex tartarica*, *Axyris amarantoides*, and others, it remains as a covering to the radicle for some time after its exit. It is, hence, easily seen that the possession, or deprivation of an epigen is of no particular significance. The two conditions in no way correspond to two distinct and different structures, but merely to very various degrees of expression of the same structure.

The correlation of the peculiarly serial zones of the radicle, dermatogen and periblem, with the more or less irregularly disposed mesenchymatous tissue of the root is effected by means of an especial cell (really, of course, a circle of cells), called by Van Tieghem, the epistele. It is the basal cell of the upper layer formed by the bipartition of the pericycle, and may be distinguished as soon as the upper layer is divided into periblem and dermatogen, a process which takes place in every cell except the basal one. Van Tieghem defines the epistele as the place where the periblem and dermatogen "se confondent." In the mature radicle, the epistele is to be distinguished from the basal cells of the plerome only by its position, and subsequent behavior. After a certain time, it undergoes transverse division, and of its two segments, the inner becomes a component of the periblem, the outer, a constituent of the dermatogen. In some cases, these two segments undergo further radial division, and the transition from dermatogen and periblem to the tissue of the root is more gradual still. In one or two rare instances, the epistele appears to consist of two or more cells, which function practically as does the simple epistele.

DETAILS OF ORIGIN AND STRUCTURE.

CARYOPHYLLACEÆ.

Dianthus sinensis. The cortical cylinder of the root possesses a diarch xylem strand separated from the two plate-like phloem strands by means of two or three layers of mesenchym. In the unmodified central cylinder, the prototracheids usually lie against the pericycle; at the place of origin of a radicle this is always the case. The entire cylinder is surrounded by endoderm, consisting ordinarily of 14-20 polyedric, or slightly rounded cells, which contain a resting nucleus imbedded in a small amount of protoplasm.

At the point of radicular origin, an uneven number of cells of the pericycle, 7, 9, 11, or even more, elongate radially, and, beginning with the central one, divide transversely to form two layers. As is normal for Dicotyledones, the inner layer gives rise to theplerome, while the outer divides again almost immediately to form the periblem and the dermatogen. At the same time, a basal cell is cut off from the histogen of the plerome, and these four cells, the three histogens and the basal cell, come to lie in the axis of the radicle (XIV:2). Concomitantly, an even number of cells of the endoderm just without the rhizogenic arc become densely filled with protoplasm, and they immediately begin to function as the epigen ("poche digestive" of Van Tieghem). Normally for *Dianthus sinensis*, the epigen persists as a single layer of cells covering the radicle until the latter reaches the exterior, when it is at once absorbed. Rarely, however, it is possible that the cells of the endoderm may divide transversely as well as radially, thus giving rise to a compound epigen. Van Tieghem has already pointed out that in some plants the cortical layers next the endoderm take part in the formation of a compound epigen. It would not be surprising, then, to find such a structure arising from the endoderm alone, as sometimes seems to be the case (XIV:2).

At this period, there is no sharp line to be drawn between the three zones, and the epistele is not yet to be discerned. The rapid elongation of the radicle, however, soon tends to

accentuate the basipetal and the basifugal division of the histogen of the dermatogen and plerome respectively, and these two zones become easily distinguishable from the periblem. At the same time, the epistele is first to be seen readily, though its formation is really anterior (XIV:1). At this period, the calyptragen, or first layer of the calyptra, is formed. Its origin is due to a single basipetal division of the dermatogenic histogen, followed by a similar division of a certain number of segments of the latter, in the present instance, four.

The further development of the radicle follows the type. By the time that the tip of the radicle has reached the exterior, the calyptra consists of three or four layers, in the outermost of which exfoliation has all but begun. The pericycle of the plerome has become set off as a single layer of elongated, prismatic cells, though the axial row of cells shows no indications of spirals. The terminal segments of the periblem, moreover, remain undivided and, as a consequence, the periblem is so far undifferentiated into endoderm and exoderm. The three histogens again assume a more nearly serial arrangement, which they maintain.

The xylem strand in the root of *Dianthus* is binary, and, according to Van Tieghem's conclusions, the arrangement of the radicles should be diplostichous. Such is normally the case; the rhizogenic arc extending from the prototracheid of the xylem strand to the primary sieve-tube of the phloem strand, thus being placed directly in front of the mesenchym. In some cases, however, one-half of the number of cells of the pericycle take part in the formation of the radicle, and the rhizogenic arc extends from prototracheid to prototracheid. At first glance, this appears to indicate biserial arrangement of the radicles and such, in fact, is what Clos had already pronounced it to be. On closer examination, however, it is seen that it is not the central cell of the rhizogenic arc, but one nearer this or that prototracheid that determines the histogenic series of the radicle. Thus, while the angle of deviation from the normal position is almost 45 degrees, nearly resulting in the opposition of rhizogenic area and of phloem,

and in a biseriate arrangement of the radicles, yet, the quadriseriate radicles never assume a perfectly biseriate disposition.

Silene otites. The structure of the central cylinder of the root is essentially similar to that of *Dianthus sinensis*. The xylem strand is diarch and is separated from the broad phloem strands by the two-layered mesenchym. The location of the rhizogenic area, and the formation of the three zones of the radicle are likewise identical. In the earlier stages of the differentiation, oblique segmentation is so frequent that it becomes almost impossible to distinguish the histogens, which, for the most part, are exactly seriate, and, as in *Dianthus sinensis*, are prolonged downward into the basal cell of the plerome.

There is no epigen in *Silene otites*. The endoderm, instead of being transformed to constitute a nourishing envelope, is quickly absorbed by the dermatogen, and the developing radicle comes to lie directly against the cells of the cortical cylinder. The calyptragen is early cut off from the dermatogen, and its comparatively large extent is no doubt due to the fact that hereafter, i. e., until the radicle leaves the root, it is to function as the digestive and absorptive layer of the radicle (XIV:4). Naturally, this function must be performed by the dermatogen for the basal portion, but, since diastasic solution and subsequent absorption are so much more active at the apex, the calyptragen may be regarded as the real organ of this process.

The differentiation of the layers of the radicle, though by no means sharp, is quite exact. In the comparatively young plerome, the axial row is already differentiated, and the pericycle is distinguishable as such at the apex of the cylinder, at least. More unexpected is the very early separation of the periblem into endodermic and exodermic layers, a step which appears in *Dianthus sinensis* only after the radicle has left the root. The significance of the early and extensive delimitation of the calyptragen has already been discussed.

At the moment when the radicle escapes from the root, its structure may be characterized, generally, as follows: The plerome consists, ordinarily, of five or six layers of typically

elongated cells, surrounded by a pericycle, whose cells are polyedral, rather than prismatic. As far as could be determined, the single histogen occupies the very apex of the plerome, and the terminal cells of the pericycle are lateral segments of it, not the derivatives of an apical segment of it, as is the case in *Dianthus sinensis*. The periblem, as stated above, is ordinarily separable into the originative layers of endoderm and exoderm. This, however, is not always true. In some radicles it is still simple at the apex, as in *Dianthus*. The dermatogen offers nothing of especial interest, except that it is composed of remarkably large, cuboidal cells, which also characterize the periblem. Its histogen, though small, is distinct, and, with its derivatives, forms a very perfect series with the histogen of the periblem and of the plerome. The calyptra consists of three layers; an inner one still in the process of formation, a middle one already well-differentiated, and an outer, earlier one, the diastasic envelope. The latter covers the entire upper half of the radicle, and is so compact that it persists intact in radicles that have pushed far beyond the root. Not a trace of exfoliation has been found in any of the sections examined. The appearance of this outer layer of the calyptra at this time is characteristic. It is of a peculiar, flabelliform shape, due to greater increase in size of the upper and terminal cells, an increase that is gradually lost toward the lower end.

The insertion of the radicles is typically diplostichous. Normally, however, the angle of deviation toward the prototracheid is so great that the paired series are almost coincident, as was demonstrated in *Dianthus*, where the deviation was, however, toward the protophloem. In one instance, moreover, the deviation is so great that the radicle is inserted directly in front of the prototracheid, which, with its arch, lies in the continuation of the axial row of the plerome.

Clos, basing his conclusions upon external evidence alone, ascribed biseriate radicles, as well as quadriseriate, to Caryophyllaceæ. Van Tieghem denies absolutely the existence of biseriate radicles, and states that Clos' error was due to lack of histological evidence. He admits, however, that externally

the radicels may appear biseriate, and that internally the angle of deviation may vary through very wide limits: virtually an admission, notwithstanding his statements, that the angle of deviation may become 45 degrees, resulting in the biseriate disposition of the radicels, just as in the case mentioned above.

Silene conoidea. The structure of the central cylinder is practically identical with that of *Silene otites*. The early stages of the radicle are essentially those of *Dianthus sinensis* (XIV:2), with the one important exception that, as in *S. otites*, the epigen is entirely lacking. The histogens of the plerome and periblem are remarkably large and distinct. The cells of the dermatogen are peculiarly cubical in shape, resulting from the fact that they function, until the separation of the calyp-trogen, as the diastasic layer of the radicle.

In the comparatively few instances noted, the insertion of the radicels was biseriate, the long axis of the xylem strand lying directly in the continuation of the axial row of the plerome, and the exterior basal cells resting exactly upon the primary sieve-tubes of either phloem strand.

Silene armeria presents the same general, histogenetic features as does *S. conoidea*. It differs merely in the diplostichous insertion of the radicels.

The Caryophyllaceæ are characterized by a diarch xylem strand, and, in consequence, by quadriseriate radicels, i. e., by diplostichous arrangement of the radicels. In this family, then, the radicle is normally opposite the mesenchymatous ray, and is limited on the one hand by the prototracheid, on the other, by the primary sieve-tube. In any genus, or species, or sometimes in a single individual, the axis of the radicle may deviate from coincidence with the ray of the mesenchym, and approach either protoxylem or protophloem. When this deviation is slight, the quadriseriate disposition is still evident, but as the angle of deviation approaches 45 degrees, the paired radicels come to lie directly over each other, either in face of the phloem, as in *Dianthus sinensis*, and *Silene armeria*, or in front of the xylem, as in *Silene otites* and *Silene conoidea*.

As Van Tieghem has demonstrated, the presence or absence of epigen in this family is not at all constant for groups higher than genera; it may be found to hold only for species. He has shown its absence in *Silene nocturna* and *integrifolia*, to which should be added *Silene armeria*, *conoidea* and *otites*, and its presence in *Dianthus viscidus*, beside which should be placed *D. sinensis*.

The histogens of the three zones of the radicle are apparently always single. In the periblem, there sometimes appears to be three, or even as many as five; these are, however, simply the undivided segments. The number of layers in the calyptra is ordinarily three, though this is entirely dependent upon the age of the radicle, and upon the presence or absence of exfoliation.

There seems to be two methods of formation for the pericycle of the plerome. In the first, in *Dianthus*, the terminal cell of the pericycle is cut off as an apical segment of the histogen, while the adjacent cells are cut off similarly from the histogenic segments. In the second, noted for *Silene*, the histogen itself occupies the apex of the plerome, and the uppermost segments cut off from it laterally go to constitute the pericycle. Van Tieghem does not make mention of two such processes in his text, but some of his drawings evidence the one or the other very clearly.

PORTULACACEÆ.

Portulaca oleracea. The xylem strand of the root is diarch in the younger plants; in the older ones, especially in the transition-region, it becomes more or less completely tetrarch. It is surrounded by a broad band of mesenchym, composed of large, polyedric cells. The phloem strand is located on either side of the mesenchym, as an elongated plate of slightly differentiated cells.

The point of origin of the radicle may be directly in face of the mesenchymatous ray, resulting in diplostichy, or it may be directly in front of the prototracheid, producing biseriate disposition of the radicles. The latter seems more often the case

in young roots, where secondary changes have not yet taken place, while in older roots, where the disposition of the elements has been altered, quadriseriate arrangement seems to be the rule. In the same maturer roots, the radicle often arise in the same plane, resulting in the formation of a compound radicle, which appears to be placed directly in front of the phloem. Such an arrangement is, however, easily reducible to diplostichy, since each component radicle of the compound one is located in front of the mesenchymatous ray.

A special, diastasic layer is lacking in *Portulaca oleracea*. The endoderm is quickly absorbed by the dermatogen, which performs this function until the differentiation of the calyptragen. The number of layers of the calyptra is ordinarily three, which extend almost to the base of the radicle.

The number of histogens in the periblem, contrary to the rule, is two; both dermatogen and plerome, however, have but a single one (XV:1).

NYCTAGINACEÆ.

Allionia hirsuta. The xylem strand is diarch, each arch consisting of four elements, united by a larger one in the centre. The prototracheids are separated from the simple pericycle by two or three layers of small cells. The mesenchym is very abundant and consists of five or six rows of small, polyedric cells, separating the large sieve-tubes of the phloem from the xylem.

The number of cells of the pericycle taking part in the formation of the radicle is nine, out of a total of forty. Two of the cells lie on one side of the prototracheid, and seven on the other. In consequence, the disposition of the radicles is diplostichous, with an inclination of about thirty degrees toward the xylem. In one instance, however, that of a mature radicle, the fifth, or middle cell, of the rhizogenic arc was directly in line with the three prototracheids, thus indicating a monostichous, or biseriate arrangement of the radicles.

As normally, the nine cells of the rhizogenic arc divide transversely to form two layers, and the upper of these two

divides again, forming the dermatogen, periblem and plerome. The fifth, or middle cell, gives rise to the histogenetic row of the radicle, and as a consequence, each zone possesses but a single histogen. The first cell of the calyptragen is cut off as an apical segment of the histogen of the dermatogen, and this gives origin to the lower layer of the calyptra, which is composed of elongate, plate-like cells, extending half-way down the radicle.

The cells of the endoderm, without undergoing any special modification, divide radially, and accompany the growing radicle as the epigen. This layer differs from the epigen of *Dianthus sinensis* in its narrow, elongated cells (XV:2), a condition, perhaps, induced by the pressure experienced in passing through the cortical cylinder. So far as *Allionia* is concerned, the epigenic layer always remains simple, contrary to the rule in some genera of this family.

Contrary to what Van Tieghem has postulated for the nature and behavior of the epistele, in *Allionia hirsuta* it appears to consist of at least two cells, one of which cuts off segments to form a continuation of the dermatogen, while the other assists in the formation of the periblem. If the epistele is but a single cell, its identity is not easily established among the two or three cells, which occupy this particular region.

At the time of the exit of the radicle from the root, it is characterized by the presence of five very distinct layers. The outermost of these, the epigen, consists of a single layer, the disintegration and absorption of which has already begun at the apex (XV:2). Below this is the calyptra, comprising four layers, the outer cells of which have undergone exfoliation even before the radicle has pierced the epiderm of the root. Beneath the calyptra and originative of it, is the dermatogen, a single layer of large, cuboidal cells terminated near the base of the radicle by the epistele. The apex of the periblem is terminated by a row of three cells, the large pentagonal histogen and its two lateral segments. From each of the latter arise two rows of cells, which become three in number sometime before the epistele is reached. The plerome consists of a

remarkably well-defined axial row surrounded by three layers of cells, in their turn enclosed in the simple pericycle. The latter takes its origin from the longitudinal division of an apical segment of the pleromal histogen.

The radicular formation of *Allionia nyctaginea* agrees completely with that of *Allionia hirsuta*. No case of genuine monostichous insertion of the radicles has been found, however.

AMARANTACEÆ.

Amarantus albus. The xylem strand of the root is diarch, and consists of eleven elements, of which the prototracheids lie directly against the pericycle. The mesenchym consists ordinarily of one layer of cells, more rarely of two. The phloem strands are small, containing only a few elements. The pericycle is simple and comprises about 20 cells.

Of the whole number of cells of the pericycle, but five commonly take part in the formation of the radicle. In all the pericycles examined, the number of cells between prototracheid and primary sieve-tube was uniformly five. Since the odd, or middle cell of the rhizogenic arc gives rise to the histogenic row of the radicle, it follows that the radicle is inserted exactly in face of the mesenchymatous ray, and forms an angle of 45 degrees with both xylem and phloem. Such an arrangement is typically perfect diplostichy, and seems to be constantly characteristic of *Amarantus albus*.

The origin of the three zones of the radicle from the pericycle is entirely normal. The endoderm, however, is not converted into epigen, but is absorbed by the calyptragen. That the latter almost solely performs the diastasic function is beyond doubt, since it is only after its differentiation from the dermatogen that the endodermis begins to disintegrate. The histogens of all three zones are unpaired. The behavior of the epistele is apparently according to the rule. The calyptra usually consists of two or three layers, the first of which, in its diastasic function, covers the upper half of the radicle.

The formation of radicles in *Amarantus retroflexus* agrees in all particulars with that in *Amarantus albus*.

Van Tieghem assigns two histogens to the periblem in *Amarantus paniculatus*, *hybridus*, *chlorostachys*, *speciosus* and *atropurpureus*. In *Amarantus albus* and *retroflexus*, there is but a single one, apparently. In the same plants he states that the delimitation of the calyptrogen takes place just before the exit of the radicle, while in those here investigated, the calyptrogen is cut off before the absorption of the endoderm.

CHENOPODIACEÆ.

Beta alba. The xylem strand is regularly diarch, each arch consisting of four to six elements. The mesenchym comprises one, rarely two layers, which passes almost insensibly into the phloem strands. The pericycle is simple, and usually contains about 40 cells.

Of the whole number of cells in the pericycle, seven are generally concerned in the formation of the rhizogenic arc. Three of these are located on one side of the prototracheid, and four on the other. In consequence, the odd, or middle cell, lies immediately to the right, or left of the prototracheid, and the angle of deviation approaches 40 degrees. No case was observed, however, where this angle becomes 45 degrees, so that diplostichy is characteristic of the radicles.

The transformation of the endoderm into epigen is a comparatively slow process. The cells enclosing the tip of the radicle are first changed, and modification then takes place in a basipetal direction. In the stage represented in figure 1, plate XVI, the cells of the endoderm at the base of the radicle are still undergoing division. From their small size and considerable number, the cells of the epigen are with difficulty distinguished from the cells of the dermatogen. Their origin is proved beyond doubt, however, by their continuity with the cells of the endoderm. Although no instance of complete bipartition of the epigen has been found, so many of its cells show transverse division, that no doubt there are cases in which it is really two-layered.

The behavior of the epistle is evolved in very considerable uncertainty. As has been already suggested for *Allionia hir-*

suta, it appears to consist of at least two cells. It may be possible, however, that primary division takes place at a time when the epistle is not to be distinguished from the adjacent cells.

The histogen of both plerome and dermatogen is always unpaired. The same is apparently true of the histogen of the periblem, though, in some cases, there appears to be a second present. The calyptrogen is early cut off from the dermatogen as a thin plate of cells, extending about half way down the radicle. The differentiation takes place slowly: the pericycle and axial row do not appear until just before the exit of the radicle from the root.

Chenopodium album. The disposition of the elements of the central cylinder is very similar to that of *Beta alba*.

Of the 20 cells of the pericycle, five are concerned in the formation of the rhizogenic arc. Of these, three are on one side of the prototracheid, one on the other side and one directly in front of it. As in *Beta*, the odd cell, the initial of the axial row of the radicle, lies immediately to the right or left of the prototracheid, and the arrangement of the radicles is atypically diplostichous.

The number of cells of the endoderm, which take part in the formation of the epigen, is normally four. As the radicle grows older, this number sometimes increases to five or six. In all cases, however, the lower part of the radicle is uniformly destitute of an especial diastasic layer (XV:4).

The epistele is very distinct, even as early as the time of origin of the epigen, and its behavior is apparently quite normal.

Van Tieghem assigns an epigenic layer to *Beta alba*, but he states that *Chenopodium album* is destitute of one. In certain genera of Chenopodiaceæ, he finds the epigen developed in very different degrees, and persisting for a very variable length of time. It may, therefore, be possible that the same genus, or the same species even, may, at one time, develop a particular diastasic layer and, at another time, be entirely destitute of such.

PHYTOLACCACEÆ.

Phytolacca decandra. The xylem strand is diarch, each arch comprising eight to ten elements. The mesenchym is a broad band of four or five layers of cells, partially enclosing the nearly circular strand of phloem.

The number of cells of the pericycle concerned in the formation of the rhizogenic arc is seven, one of which lies on one side of the prototracheid, and six on the other. The disposition of the radicle is in consequence almost perfectly diplostichous. The rhizogenic arc, as above, gives rise to the three primary layers of the radicle, two of which, plerome and dermatogen, are characterized by a single initial, while the third, periblem, possesses two histogens. The plerome is a broad cylinder, consisting of an axial row and four or five enveloping layers, the outermost of which is slowly differentiated into the pericycle. The periblem comprises but a single row of cells at the apex; below, this layer is increased to two. The calyptra is especially well-developed, consisting of three or four layers, which become as many as five or six by the time that the radicle is ready to leave the root.

The endoderm surrounding the young radicle is completely differentiated to form the epigen. Transverse divisions arise in it early, and the mature epigen then contains at least two layers.

POLYGONACEÆ.

The structure, position, and development of the radicle of *Polygonum lapathifolium* are identical in all respects with those of the radicle of *Rumex altissimus*.

Rumex altissimus. The xylem strand is tetrarch. Each arc consists of three or four elements, united in the centre by a single large vessel. The number of phloem strands is also four, separated from the xylem by two rows of mesenchym. The pericycle is simple and consists of about 40 cells.

As Van Tieghem has pointed out in the case of all quaternary roots, the disposition of the radicle is isostichous, i. e., the odd cell of the rhizogenic arc is directly opposed to the

prototracheid. If two radicles arise at the same level, they are not confluent as in the diplostichous arrangement, but stand at right angles to each other. The number of cells of the pericycle concerned in the formation of the rhizogenic arc is ordinarily seven.

The whole of the endoderm covering the radicle is modified by radial divisions into a compact epigen, which persists for some time after the radicle has left the root. The epigen never manifests any transverse divisions, and, in consequence, always remains simple.

The epistele is very prominent, existing as a cell which stains but slightly in the midst of much smaller cells, staining a deep red. The periblem possesses two initials, and is but one-rowed at the apex. Further down, it is two-rowed, and before it reaches the epistele, the number of rows becomes three. The histogen of the dermatogen and of the plerome is unpaired. The calyptragen is strongly developed, consisting of three or four rows of cells, the outer of which covers the upper two-thirds of the radicle.

CONCLUSIONS.

From the foregoing data, Van Tieghem's conclusions that the radicle proceeds always and entirely from the pericycle, and that there is but a single type of radicular formation for Dicotyledones receive new confirmation. It may, at first, seem somewhat difficult to reduce the various modifications to one type, but a careful study of each makes it evident that modification has taken place almost exclusively in the rather non-essential features of the process. Thus, while there may be considerable differences with respect to the arrangement of the radicles, the number of initials in the respective layers, the formation of the epigen, or the behavior of the epistele, there is absolute unanimity with regard to the originative layer, the method of origin, the number of primary layers, the mode of exit, etc.

The Caryophyllales are characterized by the possession of a simple pericycle and a diarch xylem strand. Exceptions to

the latter are found in the Polygonaceæ, *Rumex* and *Polygonum*, where the xylem is tetrarch. Diplostichy, or monostichy of the radicle is the rule, though isostichy is alone found in the two genera just mentioned.

The zones of the radicle are derived typically from a single initial, though in a few rare cases, *Beta*, *Amarantus*, the periblem possesses a paired histogen. The presence of a definite and well-developed calyptra is characteristic of the whole order.

As has already been mentioned, inconstancy in the formation of the epigen is characteristic of this order. The epigen is found in seven genera, and eight species, and is lacking in three genera and six species. Its instability within family, genus, and even species has also been sufficiently demonstrated.

III. THE APICAL GROWTH OF THE STEM.

HISTORICAL.

Hofmeister, in 1851, was the first investigator to study the structure of the apical region of the Phanerogams. Influenced by his researches in the Pteridophytes and Gymnosperms, he was led to conclude that the Phanerogams were likewise characterized by a single apical cell. His discoveries were made upon *Robinia*, *Elymus*, *Iris*, *Acer* and *Fraxinus*, in each of which he thought to see a single terminal cell, in some cases, cuneiform, in others, prismatic. In 1859, Hofmeister figured a terminal cell in the embryo of *Loranthus*, and of *Lathraea*, without making any definite statement as to whether the mature plant grew in the same fashion.

Caspary was the first to combat the views of Hofmeister. In his studies of Hydrillaceæ in 1858, he gives no definite expression to the apical region of *Philotria canadensis*, but, a year later, he assigned three initials to *Aldrovandia vesiculosa*, each of which is originative of a distinct layer, or zone.

Sanio, in 1864-65, found in the apex of *Hippuris vulgaris* two meristem layers, always dividing perpendicularly to the surface, which he regarded as giving origin to the leaf. Beneath these, he recognized the central cylinder, to which he

assigned no initial, although noticing the fact that both dermatogen and periblem took their origin each from a particular cell.

N. J. C. Mueller, in 1866, investigated and figured, among others, *Dianthus barbatus*, *D. plumarius*, *Fraxinus excelsior*, and *Viscum album*. To *Fraxinus excelsior*, he assigned a single initial, although his figure contradicts his statement. Douliot, from Mueller's figures, credits him with attributing three initials to *Dianthus barbatus*, and one to *Dianthus plumarius*. These drawings, which, together with those of *Viscum album*, show clearly the differentiation into plerome, periblem and dermatogen, might as easily be interpreted to represent an apex possessing two histogens. Whatever construction may be placed upon some of his figures, there can be no doubt that Mueller stood with Caspary for the existence of more than one initial in the apex of Phanerogams.

Hanstein, in two treatises, 1868, '70, first extended his researches over a large number of genera. He proved conclusively that, not only was the apex of the plant furnished with several initials, but also that these initials were to be found in the very young embryo, which Hofmeister and others had thought grew by the division of a single terminal cell. He distinguished the three primary layers of the embryo, and of the vegetative point, as dermatogen, periblem and plerome. It was by reason, however, of the constant presence of these three layers in the apex that he fell into a very considerable error. He thought that each layer, or zone, had its origin in an initial peculiar to itself, and, as a consequence, was led into attributing three histogens to all Phanerogams, a misinterpretation first corrected, as will be seen below, by Douliot.

Hanstein's opinions have been opposed by Pringsheim, Westermeier, Naegeli and others; on the other hand, his theory has been supported by Voechting, Kubin and Mueller, Haberland and Groom.

In 1890, Douliot, in a somewhat exhaustive memoir, confirms, in general, Hanstein's conclusions. While admitting regular occurrence of three layers in the apex, however, he

finds that, by reason of the community of origin of periblem and plerome, the number of initials is sometimes decreased to two, one for the dermatogen, and one common to both plerome and periblem. His investigations, which are based upon a number of genera greater than all those before studied, are conclusive and permit of the postulation of the general principle that the Phanerogams are characterized by an apical region, possessing two, sometimes three initials, but never a single apical cell.

Douliot's conclusions afford a suggestion of the possible taxonomic significance of the variation in the number of initials of the apex, and will be given here in brief.

"In the Gymnospermæ, the stem has always but a single initial cell at its summit. With Monocotyledones, the case of two initials is more frequent, that of three initials less frequent".

"In the Apetalæ, out of six examples, four have but two distinct initials; of the fifteen families of Dialypetalæ Hypogynæ studied, five possess a stem with two initials; the five families of Dialypetalæ Epigynæ have always shown three distinct histogens; finally, among the Gamopetalæ, the Plantaginaceæ alone are characterized by two initials."

"It may then be said that in the majority of Dicotyledones, the stem is terminated by three initials, and, in a small number, by two initials only; in the latter case, one initial is common to the periblem and to the plerome cylinder".

DETAILS OF THE APICAL GROWTH IN THE VARIOUS FAMILIES.

CARYOPHYLLACEÆ.

Dianthus sinensis. The apex of the seedling is characterized by two histogens, the upper of which gives rise to the dermatogen, or epidermis, the lower to both periblem and plerome. The latter is the terminal cell of the tissue beneath the dermatogen (XVII:1).

In the seedling, the periblem is always simple; it consists in the mature plant, ordinarily, of three or four layers.

Silene armeria. The three layers of the apex are more or

less sharply set off from each other. Contrary to the case in *Dianthus sinensis*, the periblem is two-rowed almost from the first. Hence, the initial of the periblem is distinct from that of the plerome, and the apical region is characterized by three histogens (XVII:2).

Silene otites. The constitution of the apical region is similar to that noted for *Dianthus sinensis*. The periblem consists of a single layer, scarcely to be distinguished, on account of its imperfect continuity, from the plerome. The two inner layers, periblem and plerome, in consequence, possess a single initial, which gives rise to its segments by longitudinal division (XVII:3).

According to Douliot, N. J. C. Mueller ascribes three histogens to *Dianthus barbatus*, and one to *Dianthus plumarius*. Hanstein assigned, in general, three initials to *Dianthus* and *Silene*, while Douliot finds in *Dianthus calocephalus* but two. There is but little doubt that Mueller erred in giving *Dianthus plumarius* a single initial, so the Caryophyllaceæ investigated may be divided into two classes, the one characterized by an apical region with three histogens, the other possessing an apex with but two. In the former would fall *Dianthus barbatus* and *Silene armeria*, in the latter, *Dianthus calocephalus*, *sinensis*, and *Silene otites*.

PORTULACACEÆ.

Portulaca oleracea. The apex of the seedling possesses two histogens, one for the dermatogen, and one common to both periblem and plerome. The latter, which is particularly large and conspicuous, forms its segments by longitudinal division. The periblem is one-layered and, except at the apex, is indistinguishable from the plerome (XVII:4).

On the contrary, the apex of a mature stem or branch shows three histogens, and three quite distinct tissue-zones. The periblem is two-rowed, and possesses its own initial. The initial of the plerome now divides transversely, instead of longitudinally as above (XVII:5). It has been impossible to make out clearly the structure of the leaf-evaginations of the apex on

account of the torsion of the tissue. They seem to have, primarily at least, but two histogens, both plerome and periblem taking their origin from the inner.

So far as could be ascertained, the apical region of the Portulacaceæ has never before been investigated, so that it is impossible to confirm by the work of others these two very diverse apex structures in the same species.

NYCTAGINACEÆ.

Allionia hirsuta. The apex of the seedling stem possesses two initials. The initial of the dermatogen is indistinct, and scarcely to be distinguished from its segments. That of the periblem and plerome is, on the contrary, extremely large and conspicuous. It gives rise by longitudinal division to segments which constitute the periblem and by transverse division to the elements of the plerome cylinder. An especially prominent feature of the apical cone is the sharp delimitation of the periblem which consists of a single layer increased to two on the sides (XVII:6).

Allionia nyctaginea is in complete accord with *Allionia hirsuta*, so far as the number and behavior of the histogens is concerned. In no case, however, was the common histogen so characteristically conspicuous, nor was there evident any such sharp differentiation of the periblem (XVII:7).

AMARANTACEÆ.

Amarantus albus. The number of histogens in the apical cone is two; as usual, one for the dermatogen, and one common to the periblem and the plerome. The latter follows the rule, and divides longitudinally to form its segments. The periblem is differentiated very late, and is never sharply delimited, except in old stems (XVIII:1).

The constitution of the apical region of *Amarantus retroflexus* is identical in all respects with that of *Amarantus albus* (XVIII:2).

CHENOPODIACEÆ.

Chenopodium album. The apex of both seedling and mature plant is characterized by the possession of two initials, one for the dermatogen, and one common to plerome and to periblem. The latter, instead of lying next the dermatogen, as is usually the case in apices having but two histogens, is situated in the next lower layer, and its lateral segments give rise to the second layer of the periblem (XVIII:3).

Beta alba. The initial of the dermatogen is not at all prominent, and is to be easily recognized only in very young apices. The plerome and periblem have a common histogen, situated as in *Chenopodium album*, in the second layer of the periblem. In apices of large seedlings, the two layers of the periblem are especially conspicuous. In very young seedlings, and in young branch-buds, there is but a single layer. Moreover, where the two-rowed periblem leaves the apex to enter the leaves, it suddenly narrows to a single row, the cells of which alternate with those of the dermatogen (XVIII:4).

The growth of the histogen common to periblem and plerome is similar to that of the initial of the dermatogen and its division is, in consequence, longitudinal.

No other genera or species of Chenopodiaceæ have so far been investigated with respect to the behavior of the apical region. To generalize from the results obtained in the two species mentioned above; the apex of the stem of Chenopodiaceæ is characterized by the possession of two histogens, the inner of which always lies in the second layer of the periblem.

PHYTOLACCACEÆ.

Phytolacca decandra. The apex belongs to the normal type, in that it possesses two histogens, one peculiar to the dermatogen and the other common to plerome and periblem. Both histogens show division in the longitudinal direction (XVIII:5).

The disposition of the periblem is two-rowed as in the Chenopodiaceæ, but contrary to the case in that family, the common initial is apparently always located in the outer layer.

The apex of the various shoot-members of the plant seems always to be characterized by identity of structure, and of behavior.

POLYGONACEÆ.

Polygonum lapathifolium. The apex of the stem possesses two histogens, and has but one layer in the periblem. The initial common to both periblem and plerome differs from that in the other families of the Caryophyllales having two histogens, in its location. Instead of being a component cell of the periblem, it occupies a position more or less superior to the latter, and simulates a single apical cell in appearance. Its division is, however, longitudinal and normal (XVIII:6).

Rumex altissimus. The common initial for the plerome and periblem behaves very differently from that of *Polygonum lapathifolium*. Division of it takes place transversely, and it gives rise, in consequence, to the two layers of the periblem (XVIII:7).

Hanstein has assigned three histogens to *Polygonum*. Douliot finds in *Polygonum amphibium* but two, the inner of which is identical in location and behavior with that of *Polygonum lapathifolium*. Notwithstanding the difference in the method of division of the inner histogen in *Rumex* and *Polygonum*, the Polygonaceæ are regularly characterized by the possession of two histogens.

CONCLUSIONS.

Of the thirteen species studied, eleven possess two initials, one possesses three initials, and one has two initials in the seedling, and three in the mature plant. In the cases of three initials, the periblem is constantly two-rowed, apparently a necessary concomitant of this structure of the apex. The converse, however, does not hold true. Of the eleven species possessing two initials, four have a two-rowed periblem, easily accounted for, however, by the various methods of division of the common initial, or by the early bipartition of the periblem itself.

The occurrence of two types of apical structure in different species of the same genus, *Silene*, and in different individuals of the same species, *Portulaca oleracea*, may possibly throw some light upon the numerous discrepancies between Hanstein's observations and those of Douliot. This fact serves to show at least that, while apical structure characterized by a single terminal cell is radically and significantly different from that possessing a number of initials, the two forms of the latter are merely different degrees of the one fundamental structure. The apex growing by the segmentation of two histogens is primitive, and that with three initials is merely a derivative, a variation of it.

The conclusions to be deduced from the above results reinforce Douliot's opinions, already quoted, to the effect that lower grades of development are characterized, for the most part, by an apex with two initials, while higher forms are distinguished chiefly by an apex with three initials. Of six examples in the Apetalæ, Douliot found four possessing two initials. Of the nine species of Apetalæ studied in this paper all have two initials in the apical region, while of the remaining five investigated, Dialypetalæ, one has three initials, one either two or three, and three have two initials.

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Readers will notice that the plates are given two numbers, viz: those conforming to the volume, and those relating to this article alone, and the latter (in parentheses) are used in the text.

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EXPLANATION OF PLATES.

THE TRANSITION FROM ROOT TO STEM.

Abbreviations: Ep, epiderm; en, endoderm; ex, exoderm; pr, pericycle; cc, central cylinder; cc', cortical cylinder; xs, xylem strand; ps, phloem strand; fs, fibrovascular strand; me, mesenchym; c, cambium; px, protoxylem; pp, protophloem; pt, prototracheids; mm, meristem; mx, metaxylem; mp, metaphloem; pc, cortical parenchyma; fc, fibrovascular strands of cotyledons; fn, fibrovascular strands of the first internode; ps', secondary phloem strands; xs', secondary xylem strands; me', medulla.

PLATE VIII (I).—*Dianthus sinensis*.

Fig. 1. Transection of the root just below the collet, showing the typical centripetal, or radial arrangement of the diarch bundle. x 660.

Fig. 2. Transection of the "tigelle" about 1 mm. above the latter; the number of the xylem elements has increased, and the prototracheids have withdrawn from the pericycle. x 880.

Fig. 3. Transection of the "tigelle" a short distance above the latter: the lateral penetration of the xylem strand by the mesenchym has begun, as also the modification of the latter into cambium. x 880.

Fig. 4. Transection of the "tigelle" in the vicinity of the cotyledons: the complete segregation of the xylem strands, and the phloem strands has been effected. x 880.

Fig. 5. Transection of the "tigelle" at the insertion of the cotyledons; the partial superposition of xylem and phloem has occurred, resulting in secantial disposition. x 350.

Fig. 6. Transection of the first internode immediately above the cotyledons: the fibrovascular system of the stem is represented by the stelar circle, composed almost entirely of procambium, except at fs, where the bundle-trace of the next pair of leaves is already somewhat differentiated. x 350.

Fig. 7. Epiderm and exoderm of the "tigelle" in transection. x 350.

Fig. 8. Epiderm and exoderm of the root in transection. x 350.

PLATE IX (II).—*Silene armeria*.

Fig. 1. Transection of the root in the region of the collet: the duplication of the xylem strand has already occurred. x 880.

Fig. 2. Transection of the "tigelle" about 1 mm. below the cotyledons: the intrusion of the mesenchym has just begun. x 460.

Fig. 3. Transection of the "tigelle" just beneath the insertion of the cotyledons: the strands of the central cylinder are in secantial orientation. x 460.

Fig. 4. Transection of the young stem: the strands of the first internode, which are destined for the next pair of leaves above, are shown at fn. x 200.

Fig. 5. Epiderm and exoderm of the root in transection. x 300.

Fig. 6. Epiderm and exoderm of the "tigelle" in transection. x 300.

PLATE X (III).—*Silene conoidea*.

Fig. 1. Transection of the root, showing the typical structure of the central cylinder. x 880.

Fig. 2. Transection of the upper portion of the root: the duplication of the xylem has begun, but the prototracheids are still in contact with the pericycle. x 880.

Fig. 3. Transection of the lower portion of the "tigelle": the duplication has reached its limit, and the mesenchym has already interposed a single row of cells between prototracheid and pericycle. x 460.

Fig. 4. Transection of the "tigelle" just below the insertion of the cotyledons: the medulla occupies the whole of the centre of the cylinder; the phloem and xylem strands are passing from the secantial to the centrifugal disposition. x 450.

Fig. 5. Transection of the stem just above the cotyledons: at fn are shown the strands destined for the leaves of the first internode; at fn' the beginnings of the strands for the second internode. x 460.

Fig. 6. Epiderm and exoderm of the root in transection. x 350.

Fig. 7. Epiderm and exoderm of the "tigelle" in transection. x 350.

PLATE XI (IV).—*Silene otites*.

Fig. 1. Transection of the root, showing the typical structure of the central cylinder. x 880.

Fig. 2. Transection of the root near the collet, showing the beginning of the duplication of the xylem elements, and, concomitantly, the withdrawal of the prototracheids from the pericycle. x 880.

Fig. 3. Transection of the "tigelle" about one-half mm. below the cotyledons: the amyliiferous endoderm is here especially prominent; the xylem strand is breaking up into secondary strands, while the mesenchym in front of the phloem is being modified to form procambium. x 880.

Fig. 4. Transection of the "tigelle" just below the insertion of the cotyledons: the central pith is well-developed; the bundles are in secantial disposition. x 300.

Fig. 5. Epiderm and exoderm of the root in transection. x 460.

Fig. 6. Epiderm and exoderm of the "tigelle" in transection. x 460.

PLATE XII (V).—*Portulaca oleracea*.

Fig. 1. Transection of the root, showing the typical structure of the stele. x 400.

Fig. 2. Transection in the vicinity of the collet; the duplication of the xylem has taken place, likewise the division of the phloem strands. x 460.

Fig. 3. Transection of the "tigelle" about 2 mm. below the cotyledons; the intrusion of the mesenchym has split the xylem into two groups. x 460.

Fig. 4. Transection of the "tigelle" a short distance below the cotyledons: the xylem and phloem strands have united at *fc* to form the strand of the cotyledons; at *c* are shown the procambial strands originative of the bundles of the first internode. x 460.

Fig. 5. Transection of the "tigelle" immediately below the insertion of the cotyledons: *fc*, fibrovascular strands of the cotyledons; *fn*, fibrovascular strands of the first internode. x 460.

Fig. 6. Epiderm and exoderm of the root in transection. x 460.

Fig. 7. Epiderm and exoderm of the "tigelle" in transection. x 460.

PLATE XIII (VI).—*Allionia hirsuta*.

Fig. 1. Transection of the root, showing the typical structure of the stele. x 400.

Fig. 2. Transection of the root: the "running out" of the central vessels is taking place, and, concomitant with it, the intrusion of the mesenchym. x 400.

Fig. 3. Transection of the root a short distance below the collet; the xylem has separated into four strands, two of which are entirely prototracheidal. x 400.

Fig. 4. Transection of the root a short distance above the latter: the prototracheids are disappearing, each phloem strand has divided to form two secondary strands, and the two remaining xylem strands have each split to form three. x 460.

Fig. 5. Transection of the lower portion of the "tigelle"; the four bundles at *fc* are destined to form the vascular strands of the cotyledons. x 460.

Fig. 6. Transection of the "tigelle" immediately below the cotyledons; at *fn* are shown the lower ends of the bundle-traces of the first internode, at *tt* the residual tracheids of the xylem. x 300.

PLATE XIV (VII).—*Allionia nyctaginea*.

Fig. 1. Transection of the root, showing the typical structure of the stele. x 400.

Fig. 2. Transection of the root, showing the disintegration of the central elements of the xylem, and the separation of the latter into two plates. x 400.

Fig. 3. Transection of the root at the beginning of the collet; the pith has made its appearance in the centre of the cylinder, and has further split the xylem into four strands. x 400.

Fig. 4. Transection of the collet, showing the secantial disposition of the xylem and phloem. x 300.

Fig. 5. Transection of the lower portion of the "tigelle", showing the two collateral bundles of the stem; pt, prototracheids; tt, residual tracheids. x 300.

Fig. 6. Epiderm and exoderm of "tigelle" in transection. x 250.

Fig. 7. Epiderm and exoderm of root in transection. x 250.

PLATE XV (VIII).—*Amarantus retroflexus*.

Fig. 1. Transection of the root, showing the type structure of the stele. x 880.

Fig. 2. Transection of the hypocotyl in the region of the "tigelle," showing the beginning of the duplication of the xylem. x 880.

Fig. 3. Transection of the "tigelle" about 1 mm. below the cotyledons in the normal transition, just below the cotyledons in the abrupt transition. The mesenchym has forced the secondary xylem strands between the secondary phloem plates. x 460.

Fig. 4. Transection of the "tigelle" immediately below the cotyledons: the bundles at fc are in secantial orientation, those at fn are perfectly collateral. x 400.

Fig. 5. Transection of the "tigelle" at the insertion of the cotyledons: the vascular strands at fc are passing over to the collateral orientation; those at fn are splitting to form the stelar system of the node next above. x 350.

Fig. 6. Epiderm and exoderm of "tigelle" in transection. x 460.

Fig. 7. Epiderm and exoderm of root in transection.

PLATE XVI (IX).—*Beta alba*.

Fig. 1. Transection of the root, showing the typical disposition of elements in the central cylinder. x 880.

Fig. 2. Transection of the collet, showing duplication of the xylem strand. x 880.

Fig. 3. Transection of the "tigelle" near the middle: the splitting of the xylem plate has already begun, as also the transformation of the mesenchym into procambium. x 460.

Fig. 4. Transection of the "tigelle" just below the cotyledons; the xylem has split transversely into two strands, likewise one of the phloem plates.

Fig. 5. Epiderm and exoderm of root in transection. x 880.

Fig. 6. Epiderm and exoderm of "tigelle" in transection. x 880.

PLATE XVII (X).—*Chenopodium album*.

Fig. 1. Transection of the root, showing the type structure of the stele. x 880.

Fig. 2. Transection of the lower portion of the "tigelle", showing the duplication of the xylem. x 880.

Fig. 3. Transection of the "tigelle" about 2 mm. below the cotyledons: the medulla, occupies the centre of the cylinder, the xylem and phloem assuming secantial disposition; at fn, a primary vascular strand of the first internode has already been cut off. x 460.

Fig. 4. Transection of the "tigelle" immediately below the cotyledons; the four cotyledonary strands have coalesced into two, and all the strands have passed into the collateral arrangement. x 660.

Fig. 5. Epiderm and exoderm of "tigelle" in transection. x 880.

Fig. 6. Epiderm and exoderm of root in transection. x 880.

PLATE XVIII (XI).—*Phytolacca decandra*.

Fig. 1. Transection of the upper part of the root, showing the beginning of duplication. x 350.

Fig. 2. Transection of the "tigelle" near the middle; the medulla has separated the xylem into transverse plates. x 350.

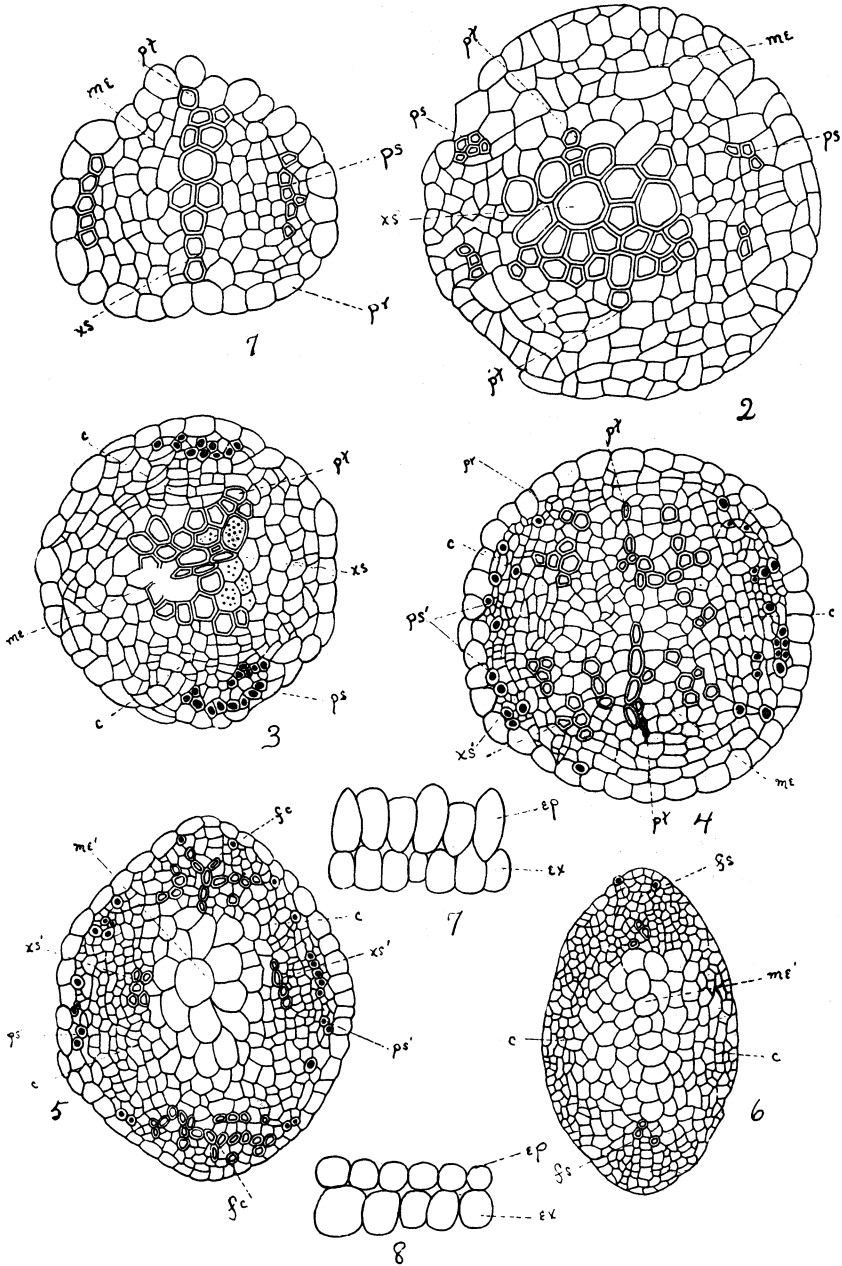
Fig. 3. Transection of the "tigelle" about one-half mm. below the cotyledons; the vascular elements are assuming secantial orientation. x 300.

Fig. 4. Transection of the "tigelle" immediately below the insertion of the cotyledons; the disposition of elements is nearly intermediate between secantial and collateral disposition. x 300.

Fig. 5. Epiderm and exoderm of root in transection. x 460.

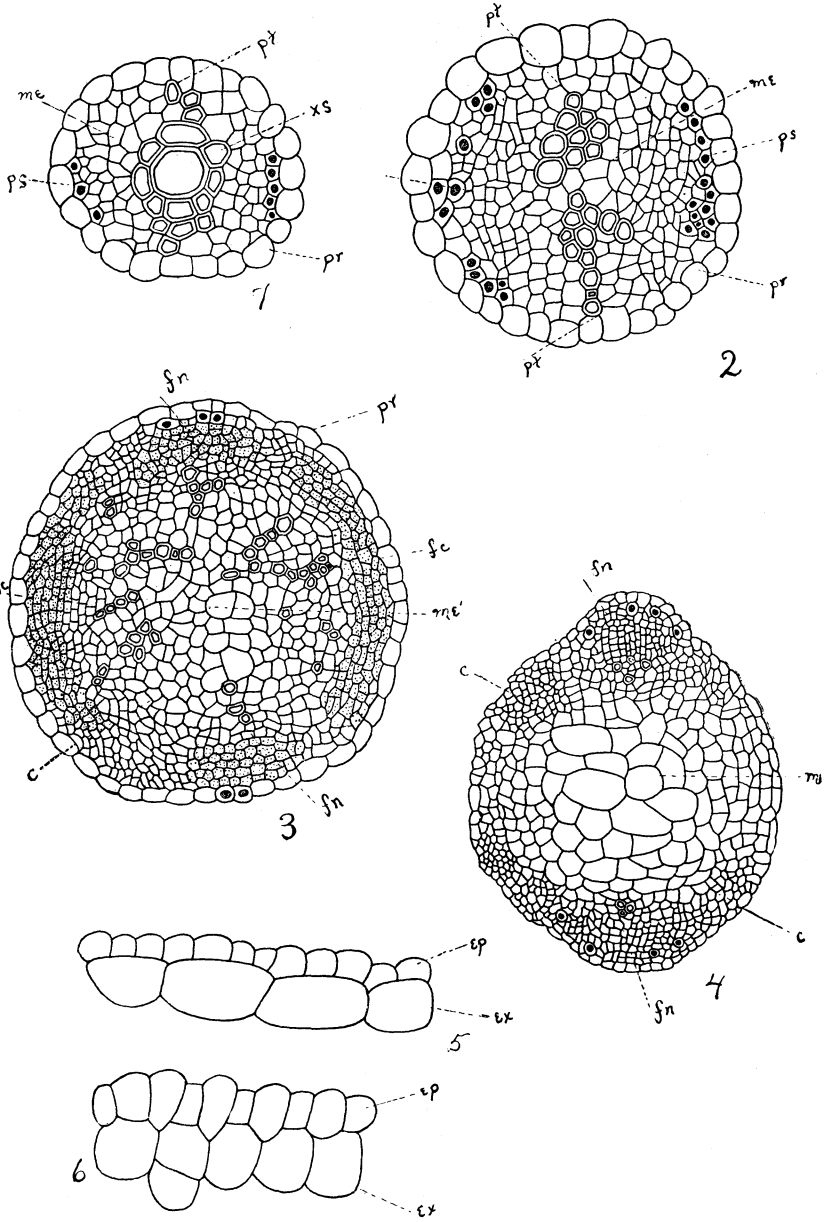
Fig. 6. Epiderm and exoderm of "tigelle" in transection. x 460.

PLATE VIII



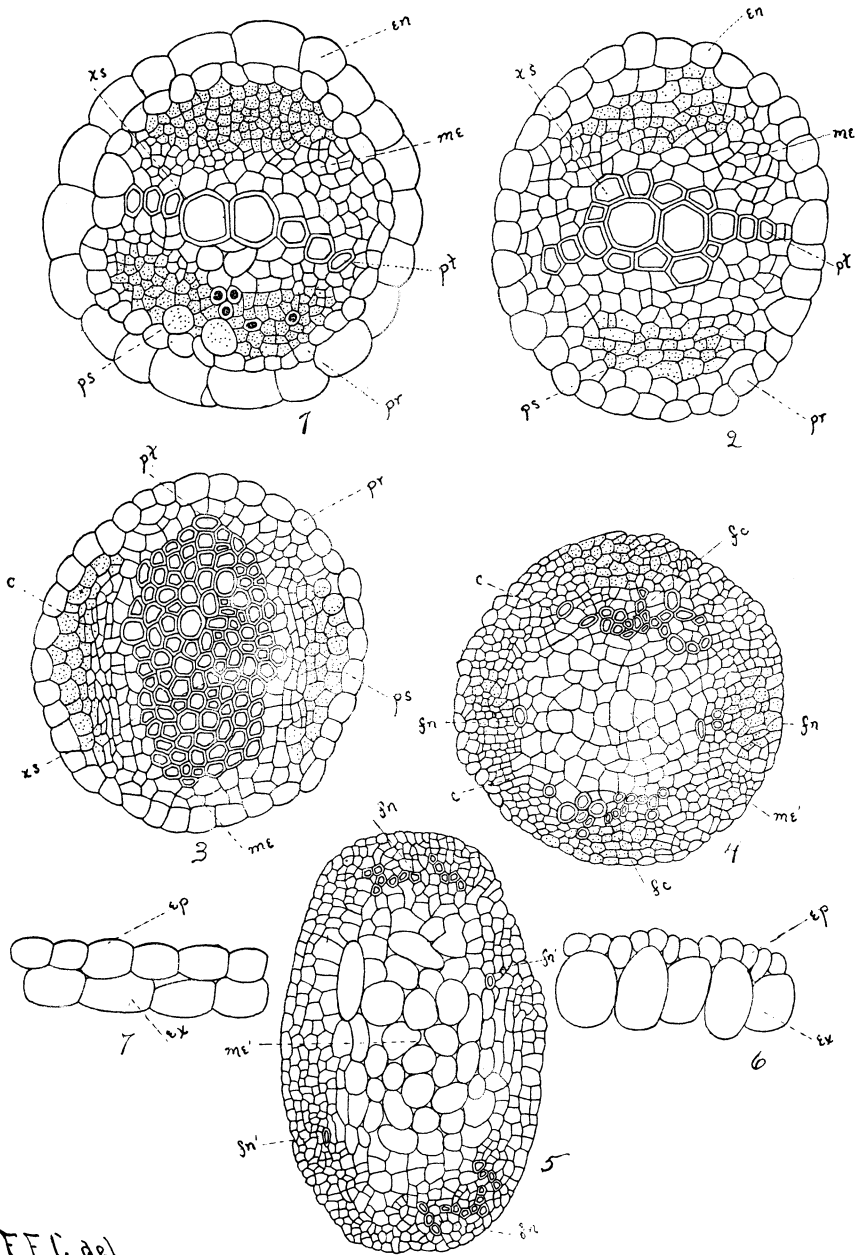
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PLATE IX



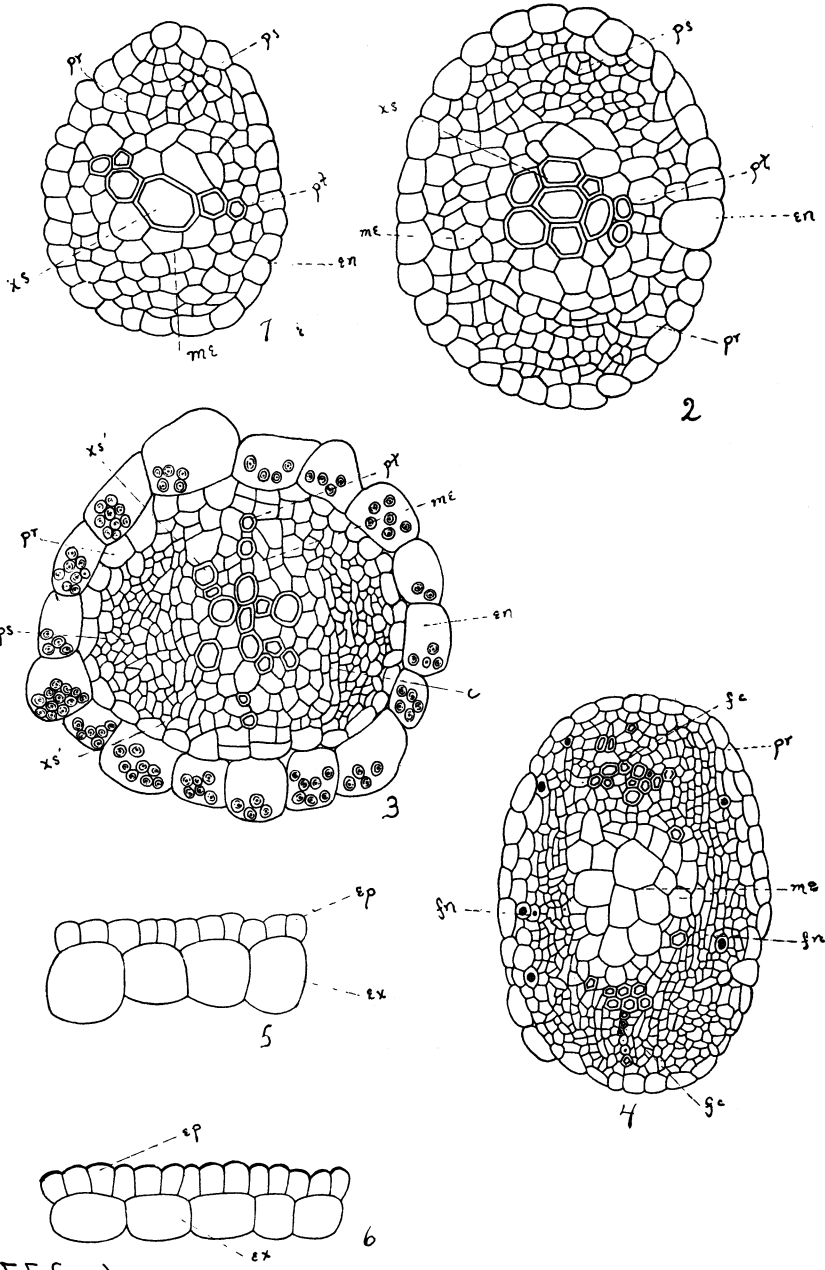
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PLATE X



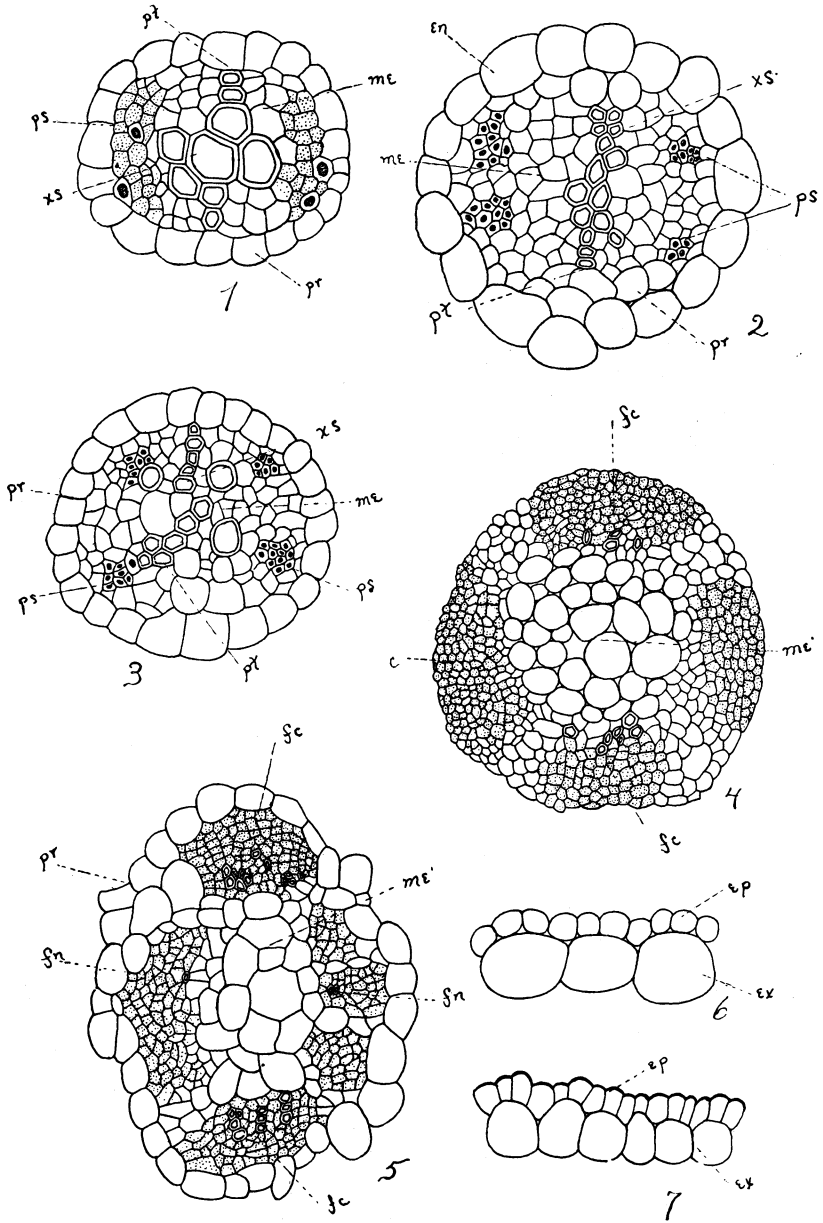
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PLATE XI



F.E.C. del.

PLATE XII



F.E.C.del.

PLATE XIII

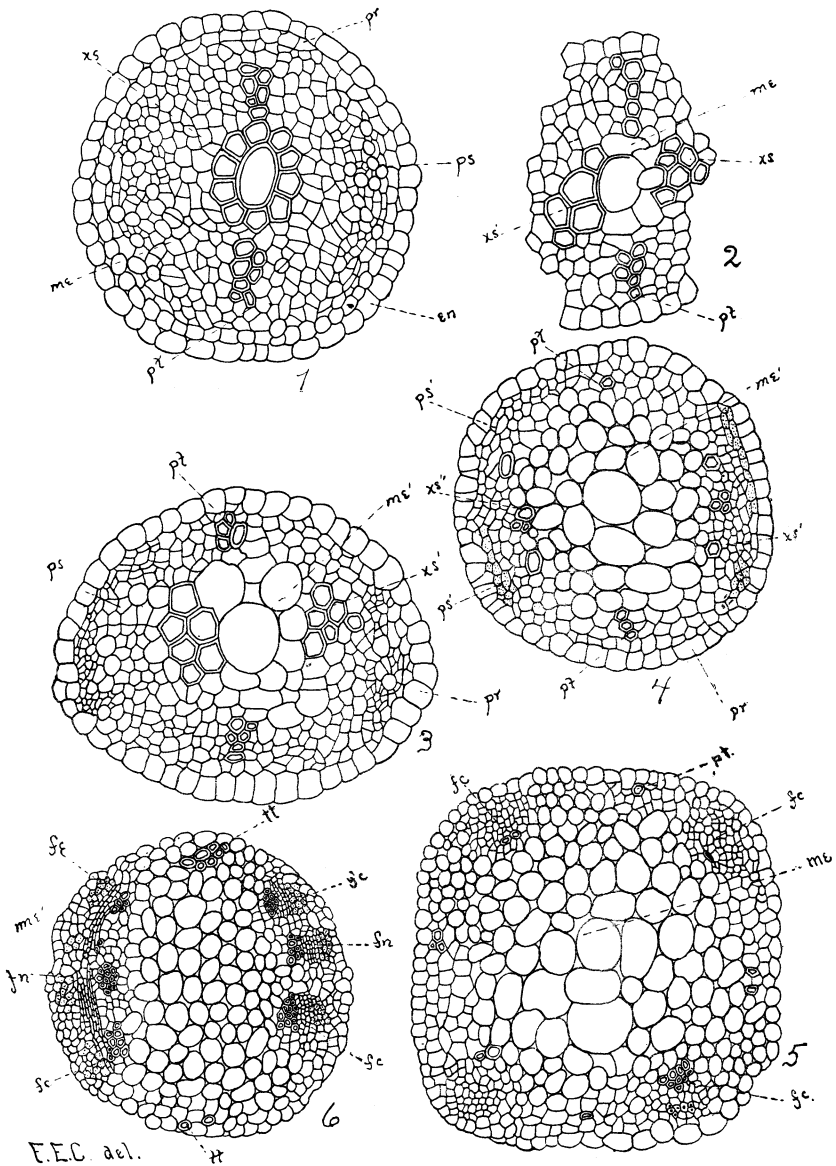
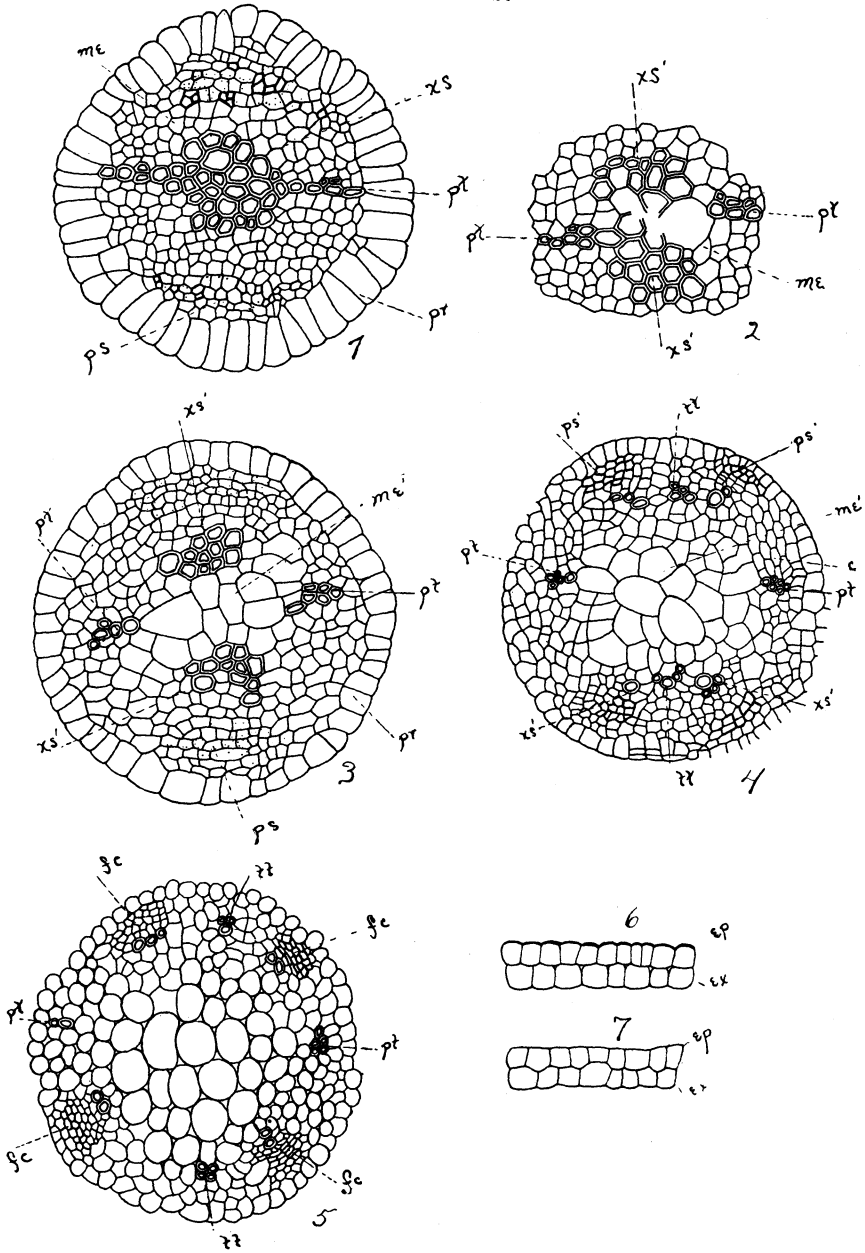
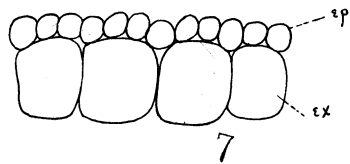
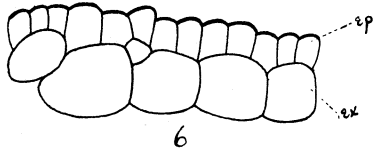
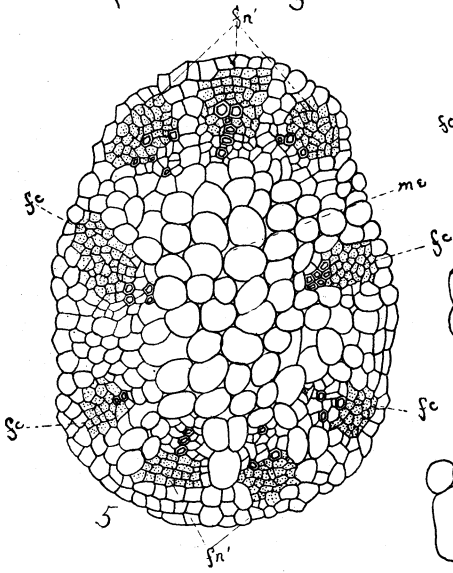
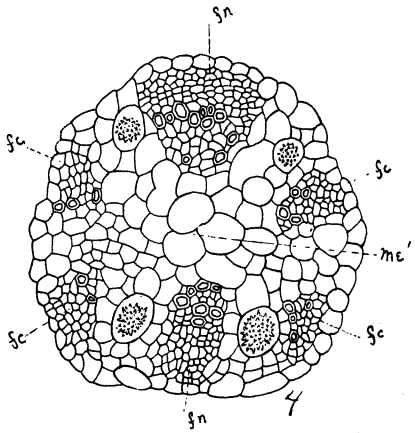
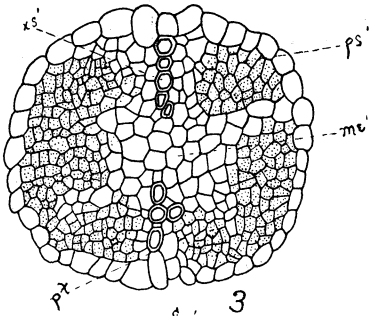
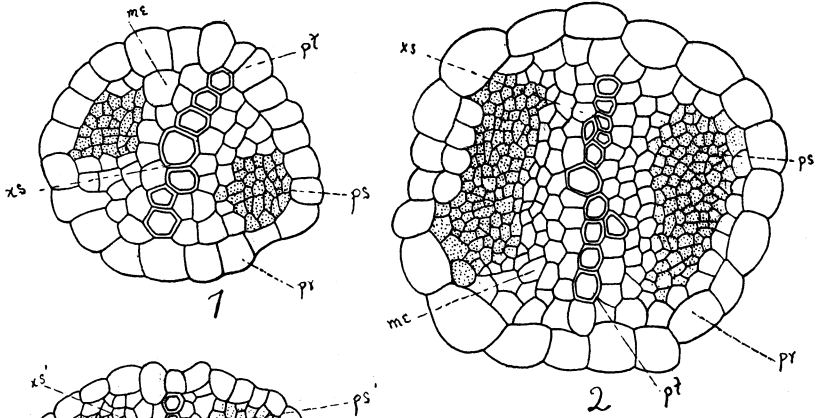


PLATE XIV



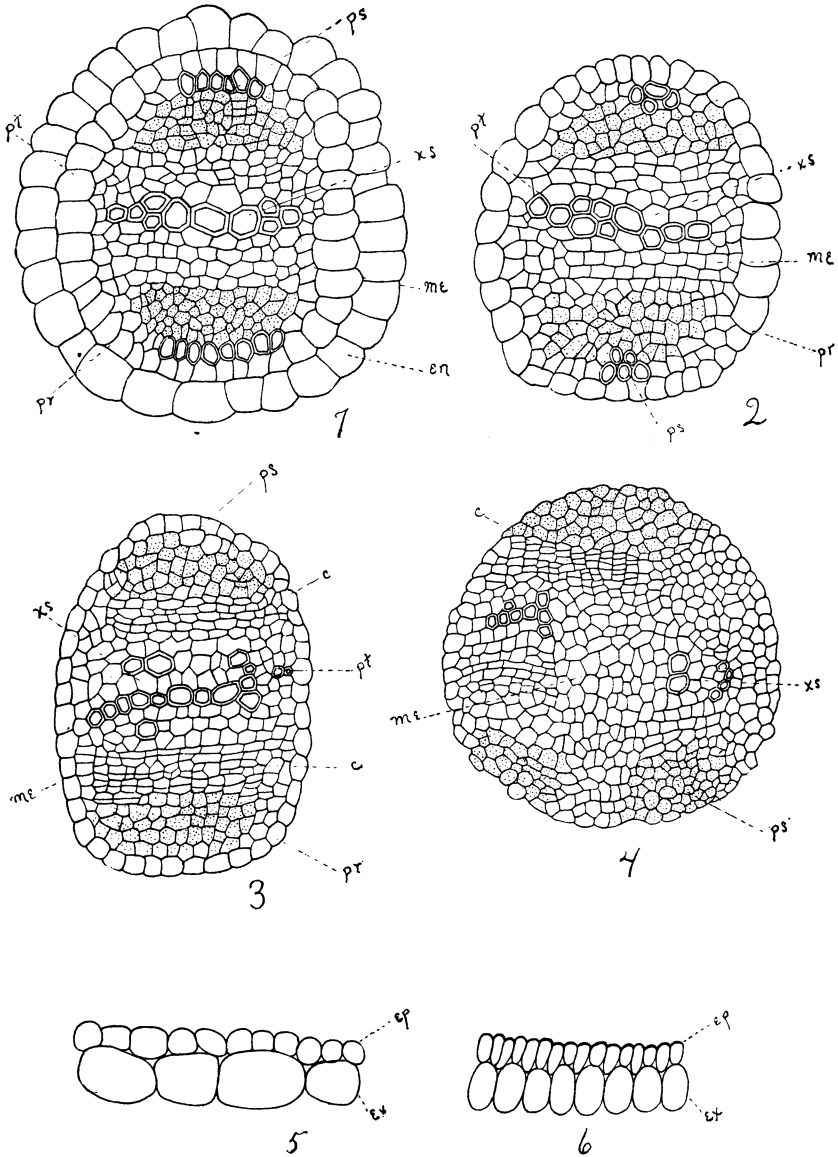
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PLATE XV



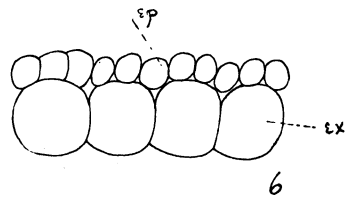
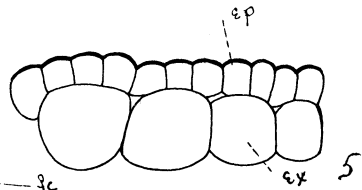
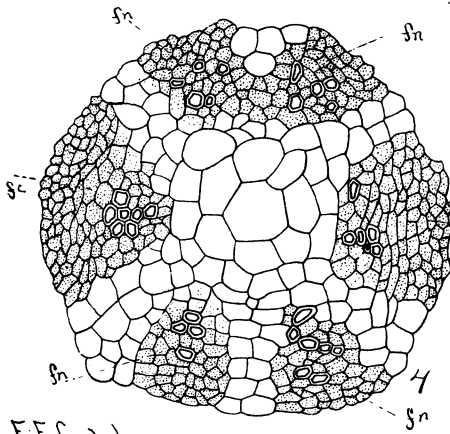
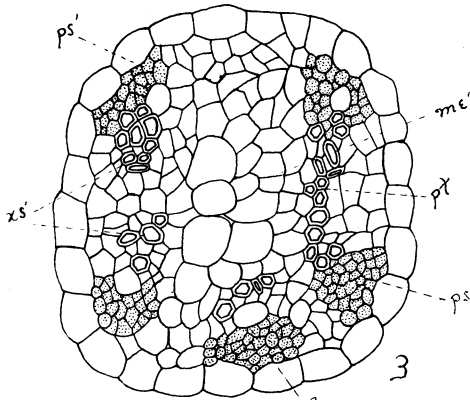
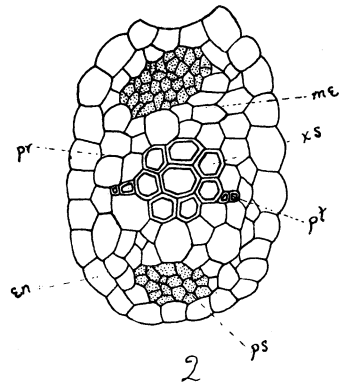
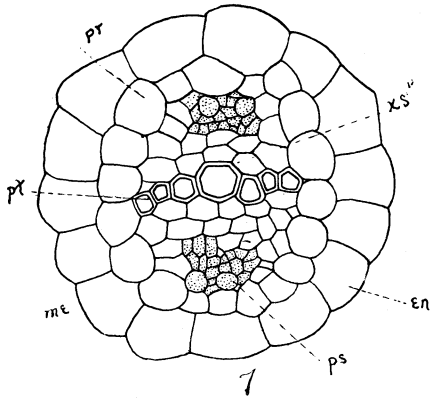
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PLATE XVI



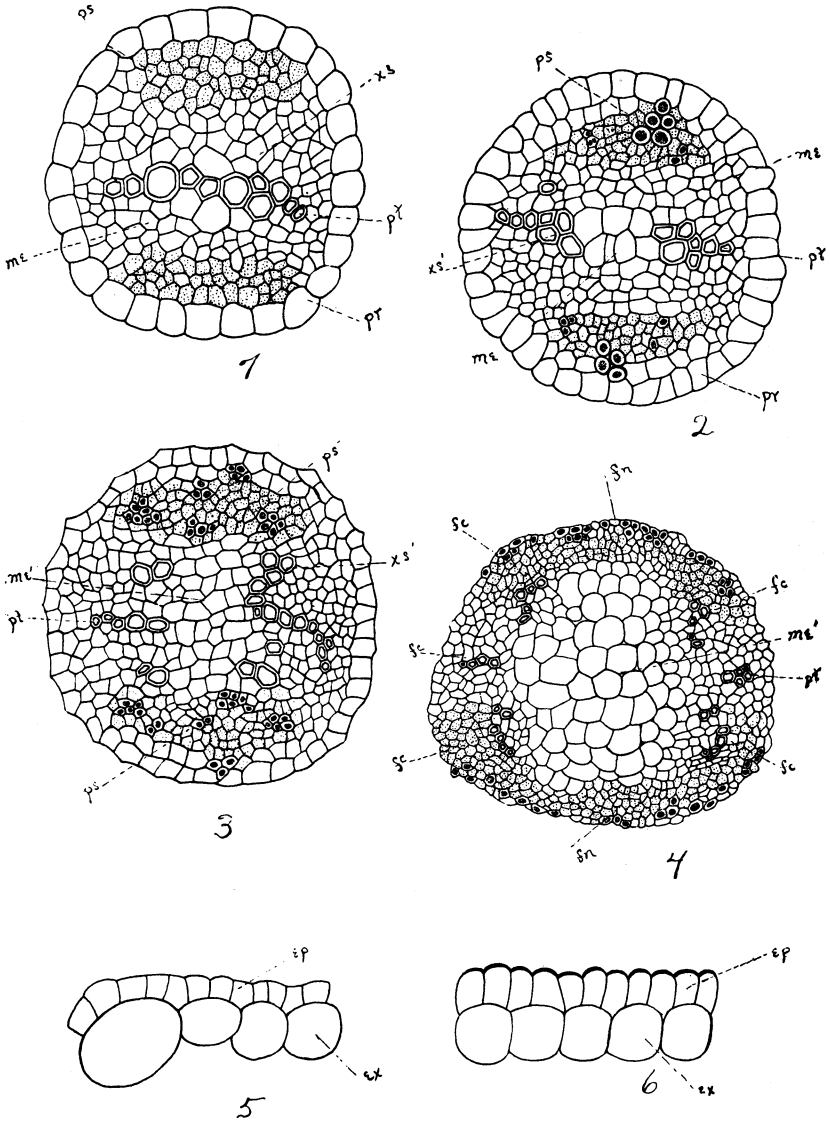
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PLATE XVII



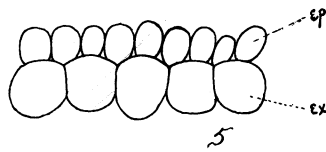
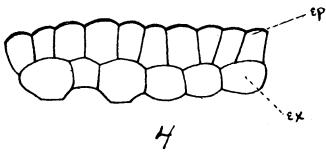
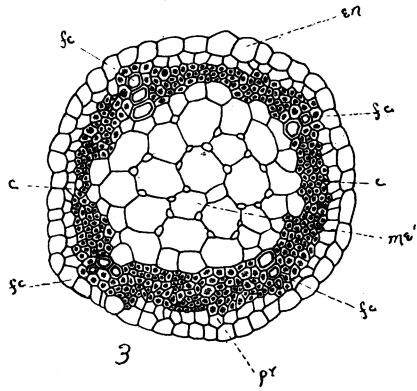
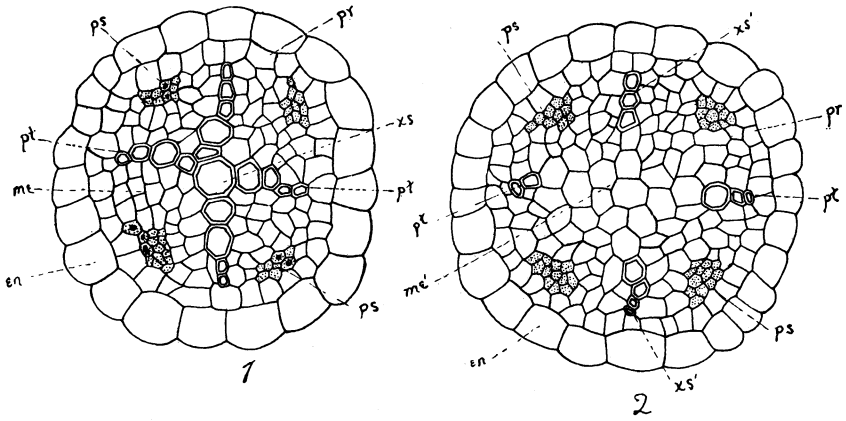
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PLATE XVIII



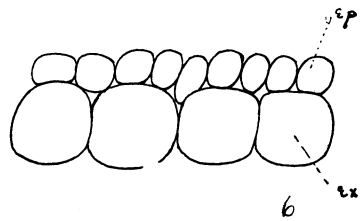
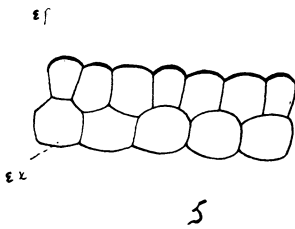
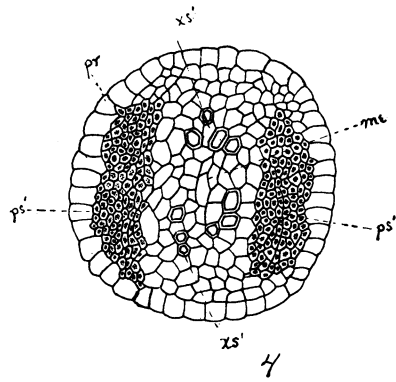
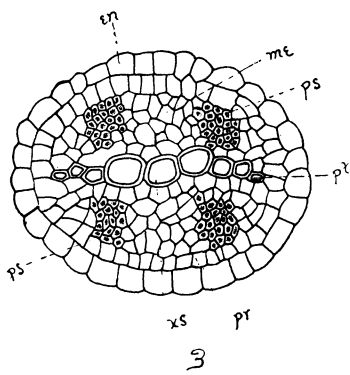
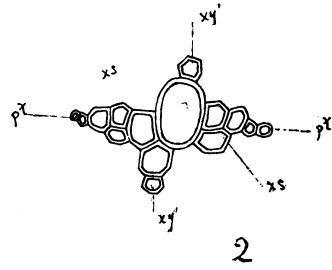
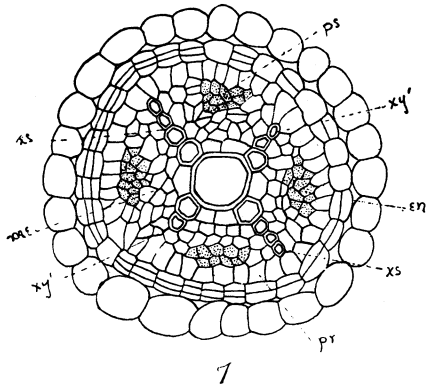
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PLATE XIX



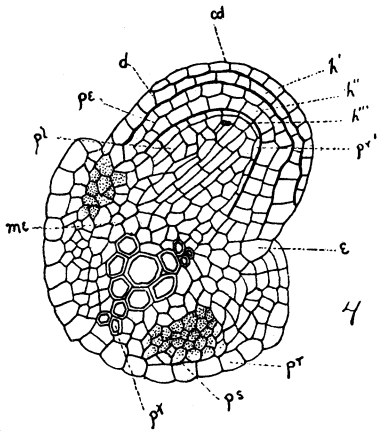
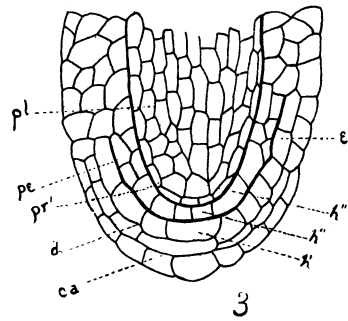
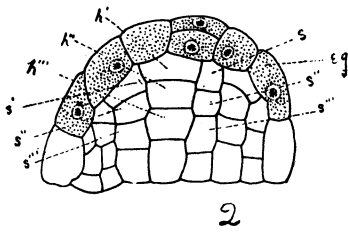
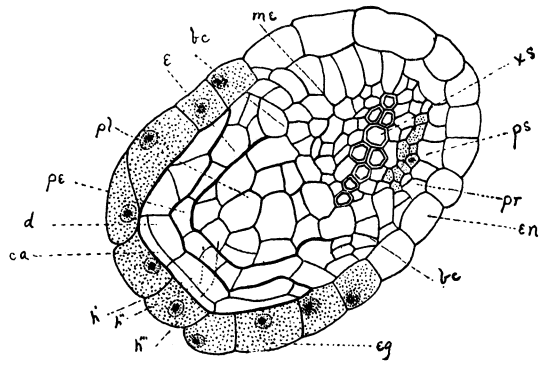
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PLATE XX



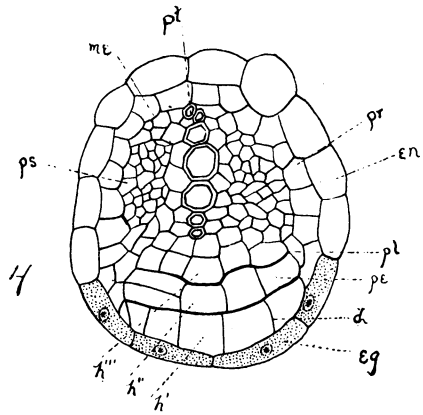
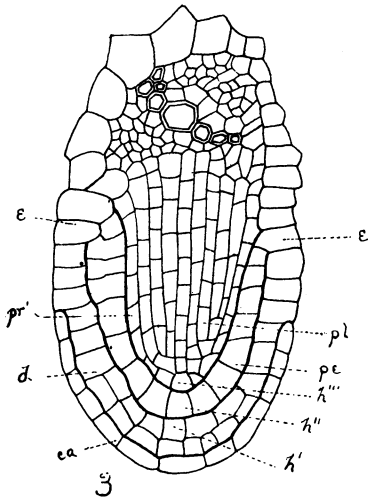
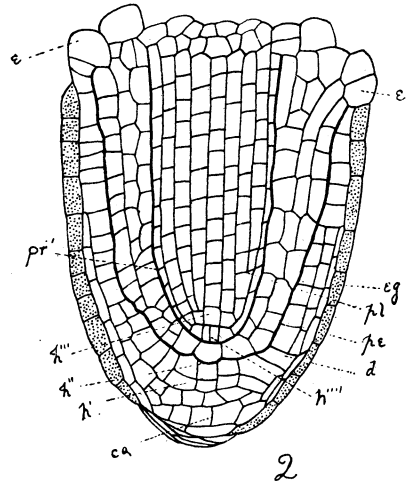
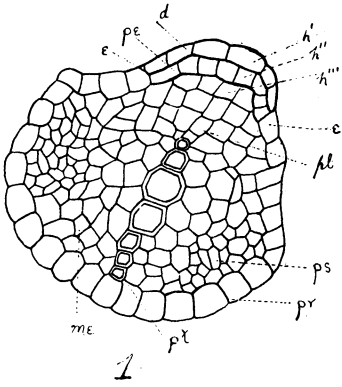
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PLATE XXI



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PLATE XXII



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PLATE XXIII

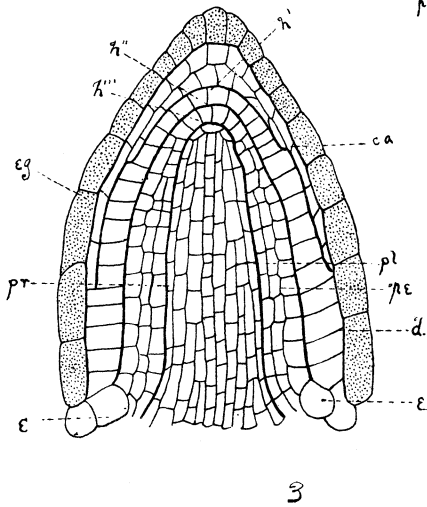
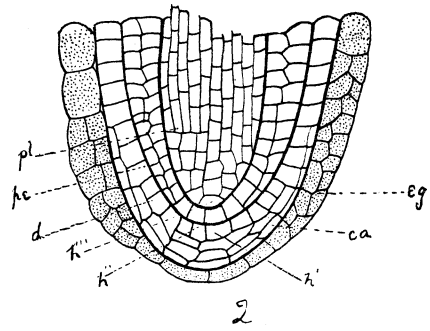
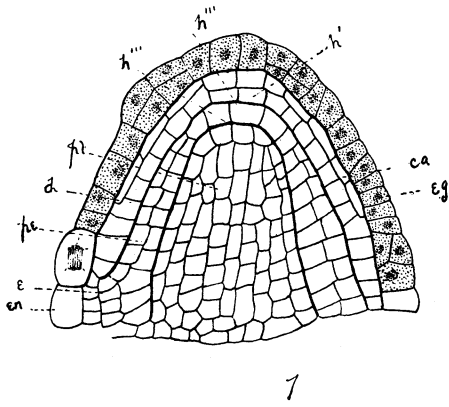


PLATE XIX (XII).—*Polygonum lapathifolium*.

Fig. 1. Transection of the upper part of the root, showing type structure of the stele. x 350.

Fig. 2. Transection of the "tigelle" near the middle; the medulla has appeared in the centre and has separated the four rays of the xylem into as many secondary strands. x 350.

Fig. 3. Transection of the "tigelle" about one-fourth mm. below the cotyledons: the phloem elements form a continuous circle, in the quadrants of which are situated the centripetal xylem-phloem strands, fc; at c is shown the interfascicular procambium which originates the first internodal stele. x 350.

Fig. 4. Epiderm and exoderm of "tigelle" in transection. x 460.

Fig. 5. Epiderm and exoderm of root in transection. x 460.

PLATE XX (XIII).—*Rumex altissimus*.

Fig. 1: Transection of the root, showing type structure of the stele: xs, primary rays of the xylem; xy', secondary rays. x 460.

Fig. 2. Xylem plate from the lower portion of the "tigelle", showing the duplication of the primary rays, and the disappearance of the secondary ones. x 460.

Fig. 3. Transection through the middle of the "tigelle"; the xylem has become uniseriate, and has assumed a pseudo-diarch character. x 460.

Fig. 4. Transection of the "tigelle" just below the cotyledons; the xylem plate has split into two, while the phloem strands have coalesced to form but two. x 460.

Fig. 5. Epiderm and exoderm of "tigelle" in transection. x 460.

Fig. 6. Epiderm and exoderm of root in transection. x 460.

THE ORIGIN AND DEVELOPMENT OF RADICELS.

Abbreviations: Ep, epiderm; ex, exoderm; cc', cortical cylinder; cc, central cylinder; en, endoderm; pr, pericycle; xs, xylem strand; ps, phloem strand; fs, fibrovascular strand; me, mesenchym; e, epistele; d, dermatogen; pe, periblem; pl, plerome; c, cambium; pt, prototracheids; mx, metaxylem; px, protoxylem; mp, metaphloem; pp, protophloem; g, digested cells of the cortical cylinder; h', histogen of the dermatogen; h'', histogen of the periblem; h''', histogen of the plerome; h''', histogen of the pericycle of the plerome; ca, calyptragen; eg, epigen; bc, basal cells of the radicle; pr', pericycle of radicle; s', s'', s''', segments respectively of histogen of dermatogen, periblem and plerome.

PLATE XXI (XIV).

Fig. 1. Transection of the root of a seedling, *Dianthus sinensis*, passing through the axis of a radicle. The three zones have become well-differentiated, and the calyptragen has been set off as a layer of five cells. The histogen of each zone is apparently single; they are, however, not serial. The epigen still consists of its original ten cells, half the number of those in the endoderm. They are very sharply set off, however, from the remaining ten cells by reason of their large nuclei and dense protoplasm. x 350.

Fig. 2. Transection of the same. The histogens of the three zones are superimposed. Their segments are extremely irregular, and the delimitation between the three zones is as yet not very evident. The epigen is composed of but six cells; the central one presents transverse division, anomalous for this species. x 660.

Fig. 3. Transection of an older radicle of the same. The radicle has penetrated the entire cortical cylinder of the root and has finally absorbed the epigen. It is still protected at the tip, however, by the two calyptral layers cut off from the dermatogen. The pericycle of the plerome is now first differentiated. x 660.

Fig. 4. Transection of the root of *Silene otites*, showing the radicle in longitudinal axial section. The epigen is lacking and the calyptragen lies directly against the tissue of the cortical cylinder. The periblem has already divided itself into two layers, originative of the endoderm and exoderm.

PLATE XXII (XV).

Fig. 1. Transection of the root of *Portulaca oleracea*, showing the young root in longitudinal section. No epigen is developed, and the dermatogen lies directly against the endoderm at this time. x 460.

Fig. 2. Transection of the root of *Allionia hirsuta*, showing the radicle in longitudinal axial section at the time when it has broken through the cortical cylinder. The terminal cells of the epigen are already dissolved, and exfoliation has begun in the calyptra. x 460.

Fig. 3. Transection of the root of *Amarantus albus*, showing the radicle in longitudinal section at the time of the absorption of the endoderm. The epigen is lacking, and the cells of the calyptra lie directly against the cortical cylinder. x 460.

Fig. 4. Transection of the root of *Chenopodium album*, showing the very young radicle in longitudinal section. The three layers derived from the division of the pericycle are very distinct. The tip of the developing radicle is covered with four cells of the endoderm modified to form an epigen. x 460.

PLATE XXIII (XVI).

Fig. 1. Transection of the root of *Beta alba*, showing the radicle in longitudinal axial section. Nearly the entire endoderm covering the radicle has been changed into epigen; near the base this process is still going on. The first layer of the calyptra has already been cut off. x 460.

Fig. 2. Transection of the root of *Phytolacca decandra*, showing a longitudinal section of the radicle. The two-layered epigen has already begun to be absorbed at the apex. x 460.

Fig. 3. Transection of the root of *Rumex altissimus*, showing longitudinal section of a radicle just ready to leave the root. The epigen still persists at the apex of the radicle. Beneath it, the calyptra has already obtained a thickness of three layers. x 460.

THE APICAL GROWTH OF THE STEM.

Abbreviations: pl, plerome cylinder; pe, periblem; d, dermatogen; h', initial of the dermatogen; h'', initial of the periblem, or common initial of the periblem and plerome; h''', initial of the plerome. All figures are magnified 480 diameters.

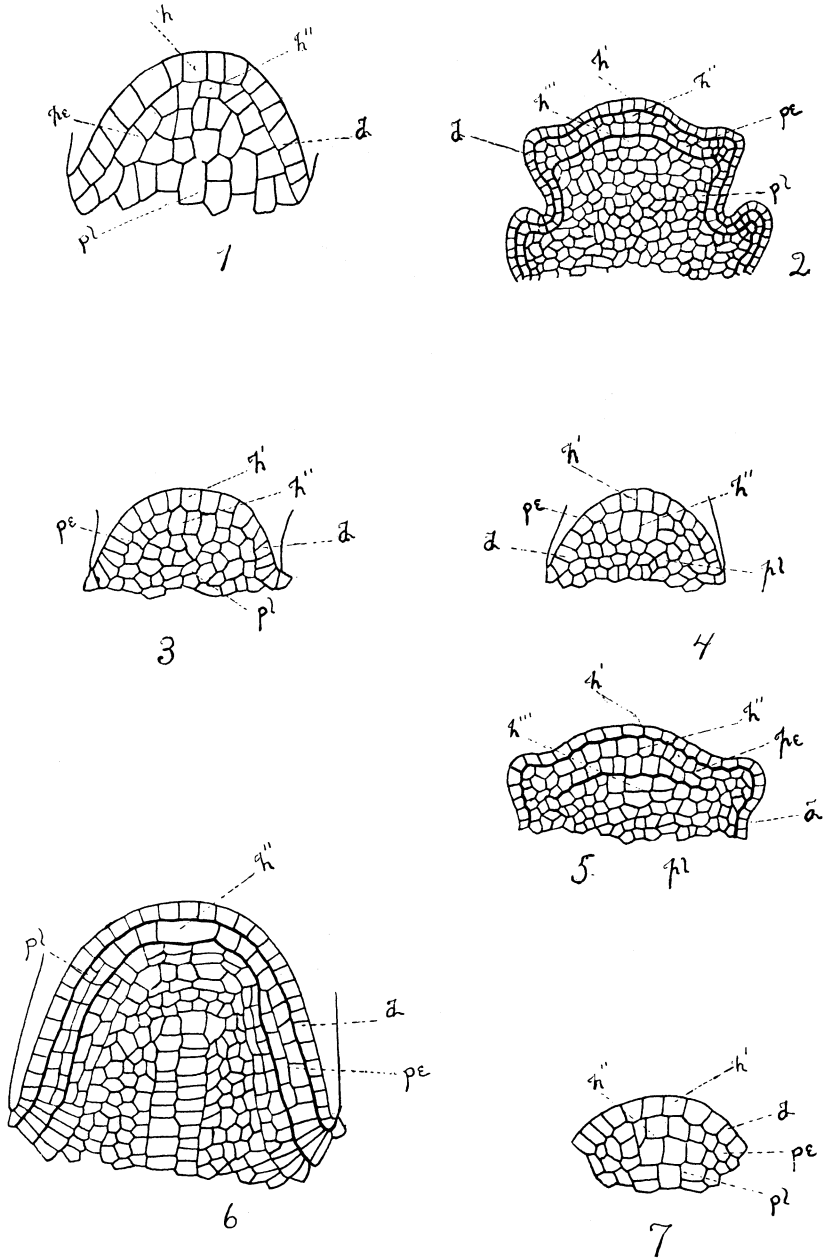
PLATE XXIV (XVII).

- Fig. 1. Longisection of the apex of a seedling, *Dianthus sinensis*.
- Fig. 2. Longisection of apex of seedling, *Silene armeria*.
- Fig. 3. Longisection of apex of seedling, *Silene otites*.
- Fig. 4. Longisection of apex of seedling, *Portulaca oleracea*.
- Fig. 5. Longisection of apex of a branch of *Portulaca oleracea*.
- Fig. 6. Longisection of apex of seedling, *Allionia hirsuta*.
- Fig. 7. Longisection of apex of seedling, *Allionia nyctaginea*.

PLATE XXV (XVIII.)

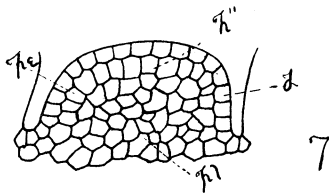
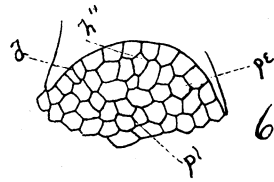
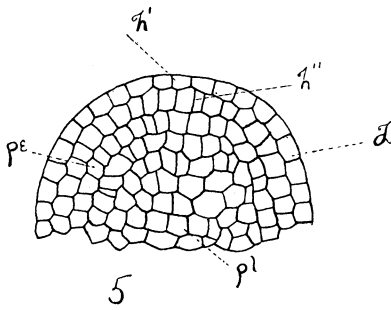
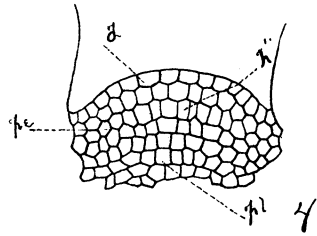
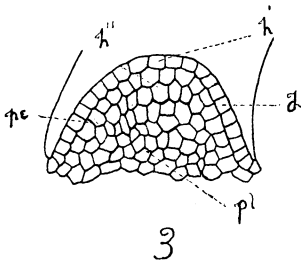
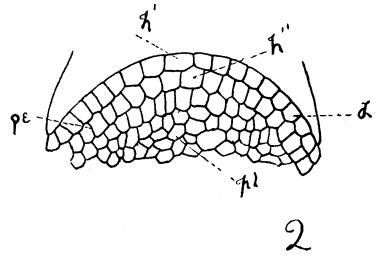
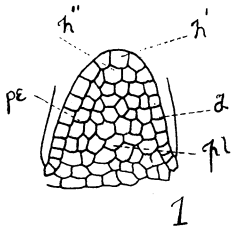
- Fig. 1. Longisection of apex of seedling, *Amarantus albus*.
- Fig. 2. Longisection of apex of seedling, *Amarantus retroflexus*.
- Fig. 3. Longisection of apex of a branch of *Chenopodium album*.
- Fig. 4. Longisection of apex of seedling, *Beta alba*.
- Fig. 5. Longisection of a flower-bud of *Phytolacca decandra*.
- Fig. 6. Longisection of apex of seedling, *Polygonum lapathifolium*.
- Fig. 7. Longisection of apex of seedling, *Rumex altissimus*.

PLATE XXIV



F.E.C. del.

PLATE XXV



F.E.C. del.